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The Journal of HEREDITY

Lamarck

"Species, then, have only a relative stability and are invariable only temporarily"

VOLUME 21 JULY, 1930 NUMBER 7

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An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

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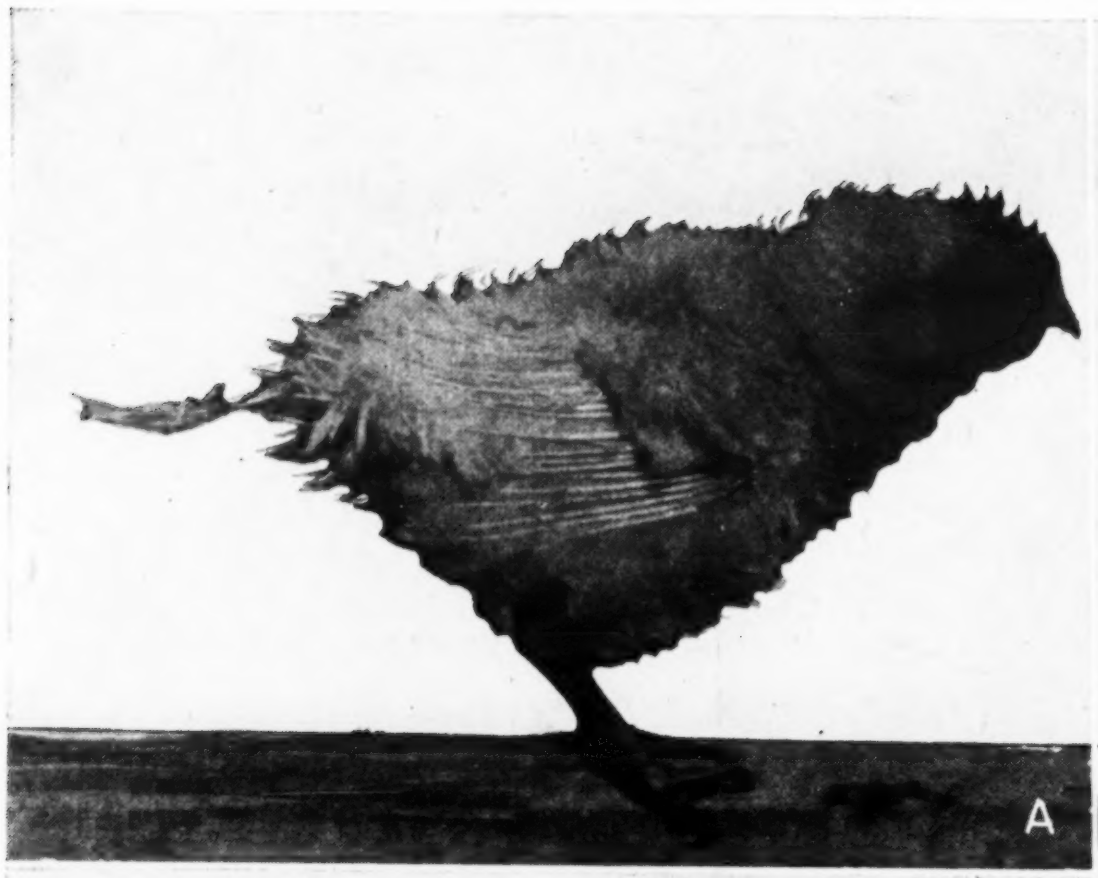
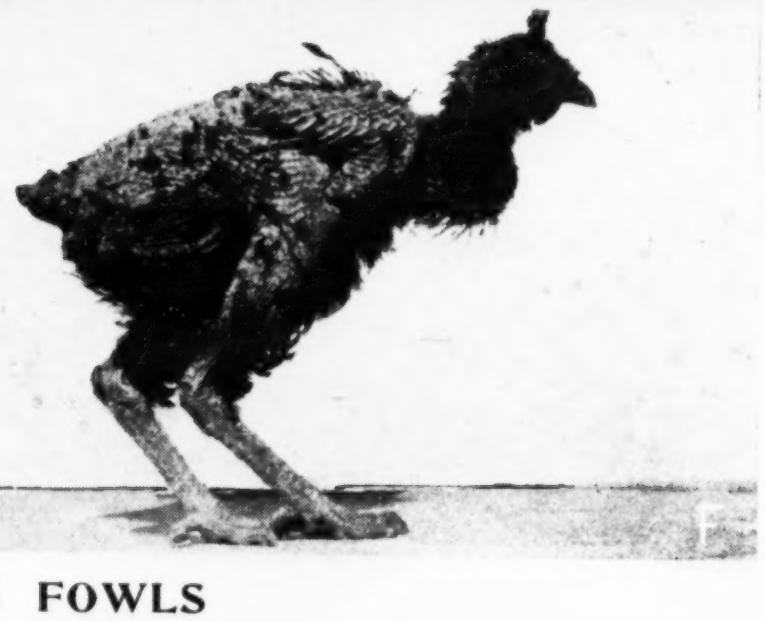




AMERICAN FRIZZLE FOWLS

Frontispiece

In breeding experiments with Frizzles three distinct types have been found with regard to the appearance of the plumage. Exhibition type Frizzles (*A*) show a relatively high grade of frizzling of all the body feathers and defective flight feathers. F_1 Frizzles (*B*, a pullet from a Frizzle-Leghorn cross) show only a slight upward curving of the feather tips. Homozygous Frizzles usually are almost bare during their first year of life (*D*, ♀ 1827; *E*, ♂ 6738); they frequently acquire a plumage with extremely narrow and curly feathers in the fall of their second year of life (*C*, ♀ 1827) which is soon lost again. A high percentage of homozygous Frizzles is sterile (*F*, ♂ 7642 two years old).

THE "FRIZZLE" CHARACTER OF FOWLS

Its Expression and Inheritance *

WALTER LANDAUER and L. C. DUNN

Storrs Agricultural Experiment Station, Storrs, Conn.

THE so-called Frizzle fowl is one of the most striking among the many breeds and varieties of chickens. This breed owes its name to a peculiar upward-turning, curling or frizzling of the feathers of the body plumage.

Geographically the Frizzle fowl shows an almost cosmopolitan distribution. Various authors witness its occurrence among the native flocks of Southern Asia and East India, Java, Sumatra, Ceylon, the Philippine Islands, Guam, Mauritius, Mozambique, the West Indies, Surinam, Guiana, Asiatic Russia, and other parts of the world. It seems safe to conclude from this universal distribution that the unusual appearance of the Frizzle fowl aroused man's interest and fancy long before actual records of its appearance were preserved. Aldrovandus, writing in the sixteenth century, referred to the Frizzle fowl as the "monstrous" hen; Linnaeus named it *Gallus pennis revolutis* and Brisson described it as *Gallus crispus*.

Reports, however, of scientific work concerning the Frizzle fowl are very scarce and incomplete. Davenport[3] reported in 1906 a cross which he had made between Frizzle hens and a Silky rooster. He characterized his frizzled birds as follows:

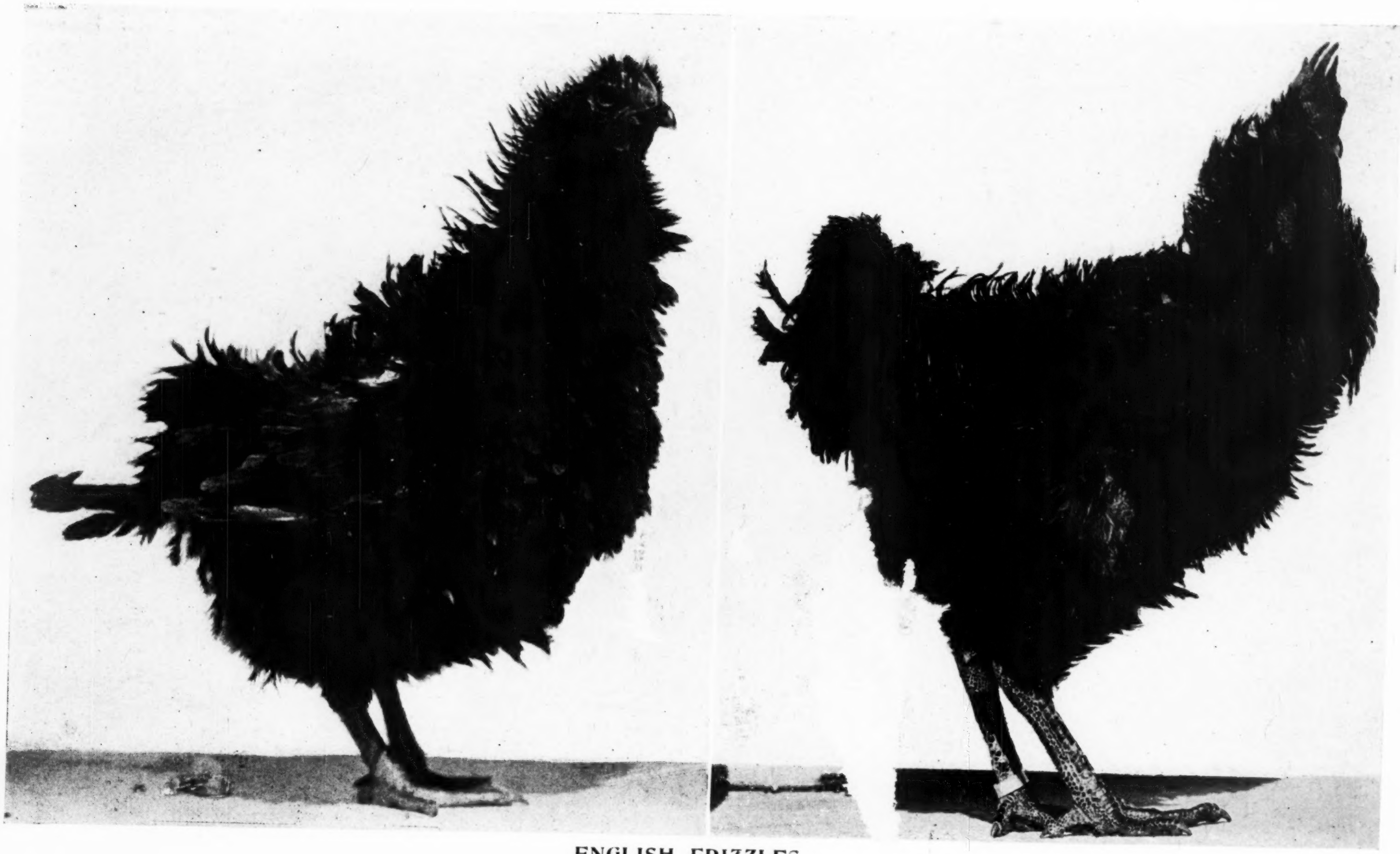
> In the Frizzles the contour feathers have the shaft curved so that its outer surface becomes concave. This is most striking in the neck region, where a ruff is formed. The wing primaries are modified in another direction, since in them the barbs, in groups of 4 to 8, are twisted in corkscrew fashion about their own axis and through 180° or more; consequently the gray surface, which is normally next to the body, comes to lie outermost. * * * The barbs of the remiges of the Frizzles are mostly short, and in some cases are lacking altogether, being easily broken off.

Davenport's cross resulted in a progeny of ten mature birds of which six were frizzled, while four had a normal plumage. Assuming that all four Frizzles used for the cross were heterozygous, Davenport concluded that the differences between frizzled and non-frizzled are determined by a single pair of factors, frizzling being the dominant allelomorph. Davenport refers to frizzling as a "positive character added to the perfect feather," and he thinks that this is a "progressive" variation as compared with the "primitive" condition of the normal feather or the "retrograde" type of the Silky feather. The same cross of Frizzles and Silkies had been made already by Tegetmeier who described the offspring from his cross as "white frizzled negro fowls."

This appears to be all the available experimental evidence concerning the inheritance of frizzling, but Crew[2] and Wriedt[9] have stated that the Frizzle character acts as a lethal in homozygous condition. Crew, in fact, says: "In the case of the fowl lethals are to be found in the Frizzle, for it would seem that the homozygous frizzled bird does not appear, . . ." These statements are probably founded on the experience of poultry breeders that Frizzle fowls do not breed true but always produce some normal progeny.

We started experiments with Frizzle fowls in 1927 with the purpose of verifying, if possible, the lethal nature of the Frizzle gene. At this time we obtained a few Frizzle pullets and two Frizzle roosters from two different

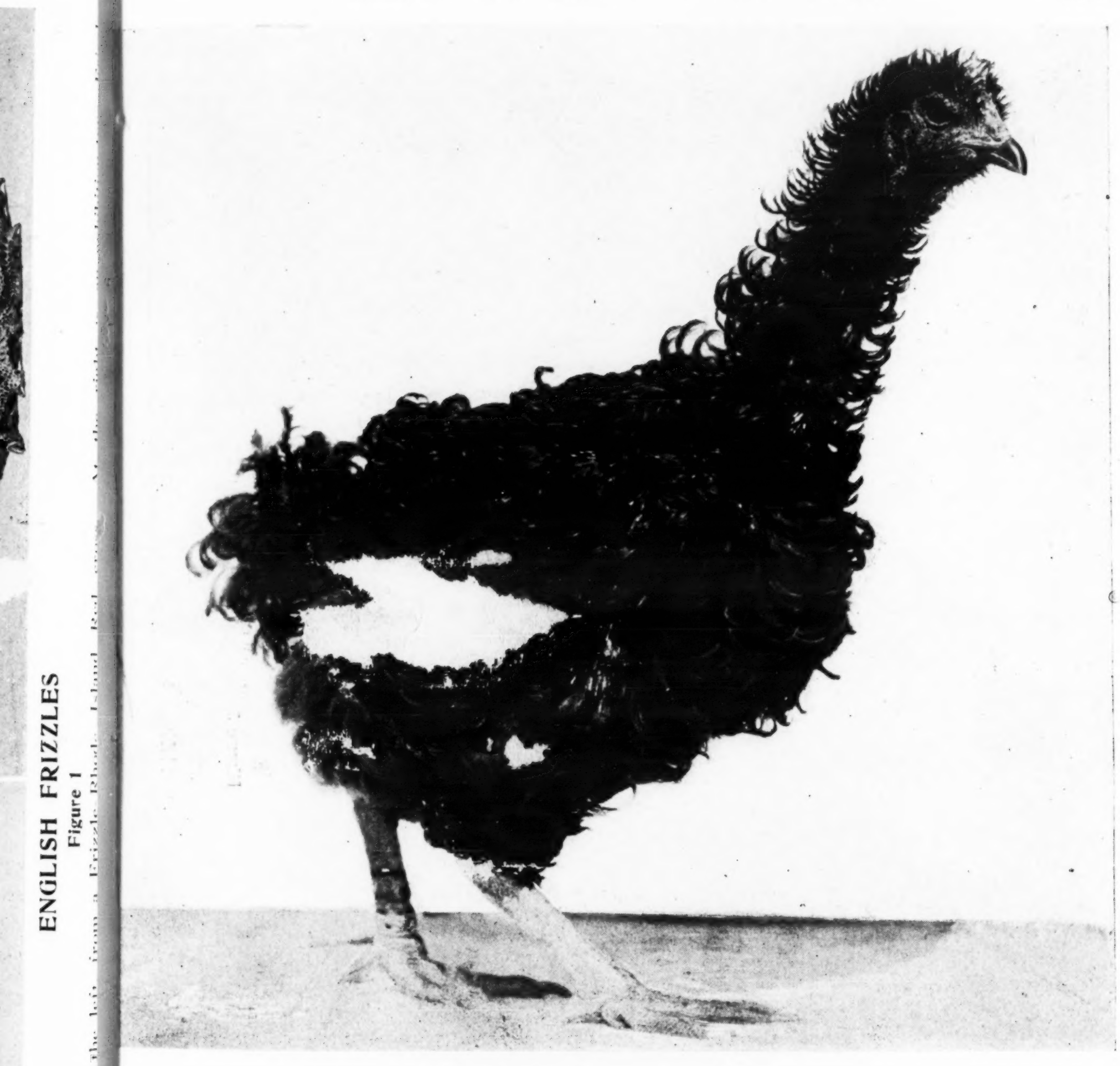
* A preliminary report of this work has been published in Director's Report, Storrs Agricultural Experiment Station, *Bulletin 162*, 1929.



ENGLISH FRIZZLES

Figure 1

An F$_1$ Frizzle pullet (♀ 7842), is shown at the left, from a Frizzle Black Island Red cross. At the right is a typical Frizzle



ENGLISH FRIZZLES

Figure 1

An F₁ Frizzle pullet (♀ 7842), is shown at the left, from a Frizzle (Rhode Island Red ♂ ...) × Mongolian Frizzle (♀ ...) mating. The Frizzle pullet is shown at the right, from a Frizzle (Rhode Island Red ♂ ...) × Leghorn (♀ ...) mating.

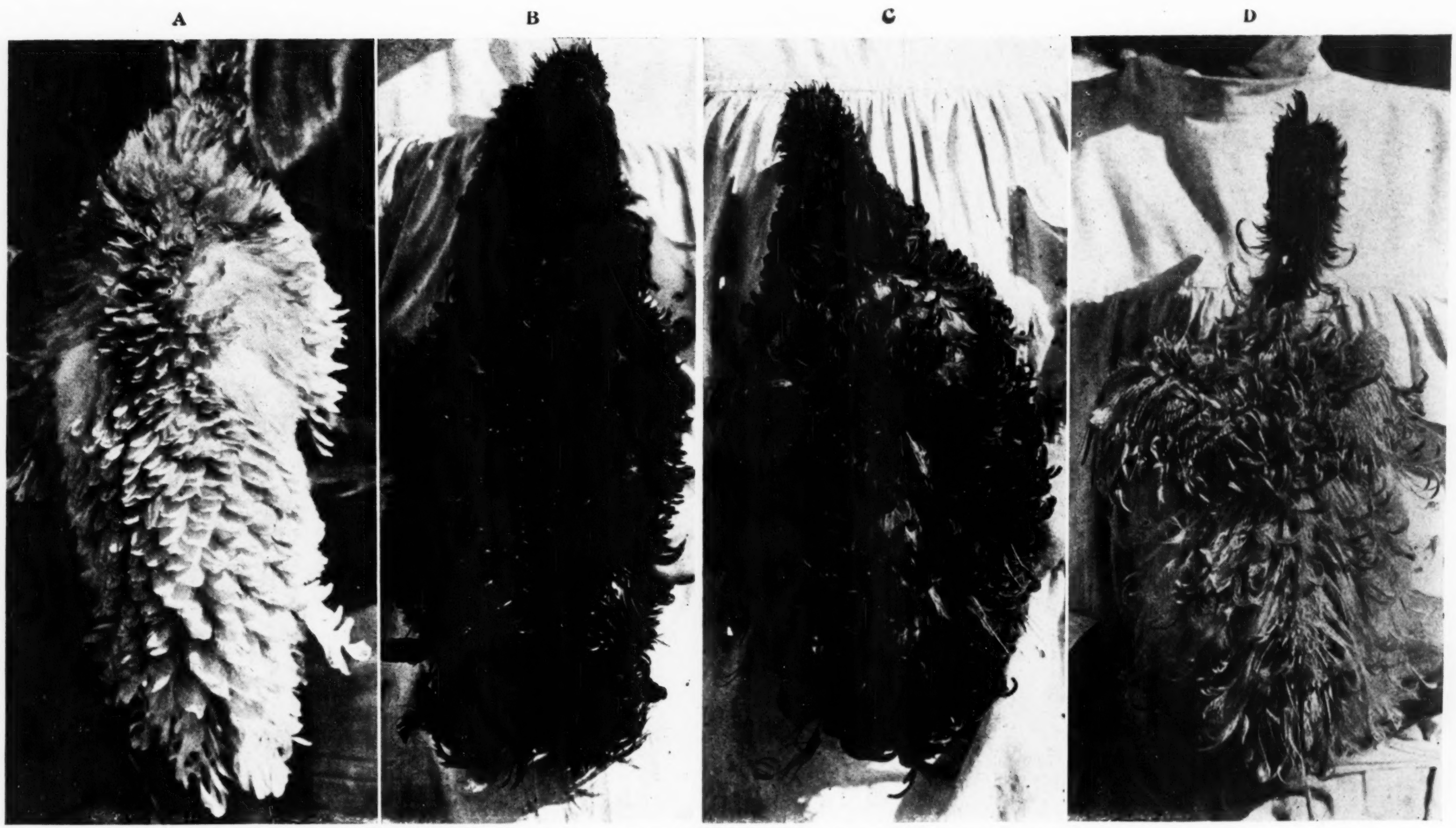
A HOMOZYGOUS ENGLISH FRIZZLE

Figure 2

This hen (♀ 1824) is an example of the degree of curling of the feathers found in homozygous frizzles. The frizzling gene in the pure state is not lethal, as heretofore supposed, but the homozygous chicks are more delicate and harder to raise than chicks carrying the normal recessive factor.

sources in this country.* In order to increase our stock these birds later on were crossed to Leghorns, and a part of the F_1 Frizzle pullets from these matings were crossed with a Bare-neck rooster. Throughout this paper we shall refer to the original stock which we purchased as well as to the Frizzle lines derived from them as "American" Frizzles. In 1927 we also purchased

*Mr. M. E. Coe, Mississippi Agricultural and Mechanical College, and Mr. A. E. Cutler, Putnam, Conn.



HETEROZYGOUS AND HOMOZYGOUS FRIZZLE FOWLS

Figure 3

Dorsal views of various types of Frizzle fowls: *A*, an American F_1 Frizzle pullet (from a Frizzle-Leghorn cross); *B*, an English exhibition-type Frizzle cockerel; *C*, a homozygous English Frizzle pullet (♀ 2007); *D*, a homozygous American Frizzle hen (♀ 1828). The difference between the F_1 Frizzle and the exhibition-type is believed to be due to the presence of other genes than that determining frizzling.

from one of the leading Frizzle breeders in England* four females and a male of a red Frizzle strain. We added to this mating normal Rhode Island Red pullets in order to increase our stock. To these Frizzles and their descendants we shall refer as "English" Frizzles. Since we did not recognize definitely the homozygous type of Frizzles until 1928, the present report is based only upon the breeding data obtained during 1929, and the incubation data for 1929 and 1930.

Preliminary experiments in 1927 and 1928 showed that all of the Frizzled fowls from both sources were heterozygous for a gene which behaved as a single dominant to normal plumage. Matings of an English Frizzle male by normal females produced 18 frizzled and 23 normal progeny; an American Frizzle male by normal females gave a progeny of 22 Frizzles and 22 normal chickens. Matings between English Frizzles in 1927 (Edinburgh) produced 36 frizzled and 13 normal progeny, and in 1928 (Storrs) 40 Frizzles and 15 normals. These obviously resembled 3:1 ratios so closely as to make the assumption of lethal action of the Frizzle gene when homozygous very doubtful. The incubation records of Frizzle × Frizzle matings in 1927 and 1928 also failed to show the high mortality expected if 25 per cent of the embryos died from action of a lethal gene. We concluded tentatively that the Frizzle gene had no lethal action in embryonic stages and that another explanation should be sought for the fact that Frizzle fowls kept and offered by breeders were heterozygous. The first suggestion of this explanation was our discovery among the progeny of Frizzle × Frizzle matings of many weak, small chickens, almost bare of plumage. Two such were among the American Frizzles bred to a normal male in 1928, and these produced only frizzled offspring, suggesting that the homozygous Frizzle fowl hatches but either dies early in life or is eliminated by the breeder because of its defective plumage.

Different Types of Frizzling

In the course of our breeding work it became evident that we were dealing with different types of frizzling, and, in order to facilitate the presentation of our genetic data, these different types will be described first. Representative specimens purchased from fanciers as foundation stock for our experiments are shown in Frontispiece (*A*) and in Figure 1*B*. They show a fairly high degree of curling of all the body feathers, while the feathers of wing and tail have a ragged appearance and frequently lack a part of or all the barbs. These birds, which genetic tests have shown to be heterozygous, we shall call "exhibition-type" Frizzles since they are of the kind generally shown by fanciers in poultry exhibitions. If such exhibition-type (and also homozygous) Frizzles are bred to non-frizzled chickens, the frizzled F_1 animals show a lower grade of frizzling (Frontispiece *B* and Fig. 1*A*). In such birds the feathers of the body plumage are only curved upward at the tip without curling. The flight feathers more frequently approach a normal appearance. The fact that out-crosses of exhibition-type Frizzles result in a progeny with a much lower grade of frizzling indicates that the exhibition-type of frizzling has been produced by selection and that it depends in its expression upon the presence of other genes besides the gene for frizzling. Finally, the homozygous Frizzles (Frontispiece, *D, E, F* and Fig. 2) are strikingly different from either of the two

English exhibition-type Frizzle cockerel; *C*, a homozygous English Frizzle pullet (♀ 2007); *D*, a homozygous American Frizzle hen (♀ 1828). The difference between the F_1 Frizzle and the exhibition-type is believed to be due to the presence of other genes than that determining frizzling.

*Major G. T. Williams, Perranwell, Cornwall. These were delivered to one of us (L.C.D.) in the spring of 1927 while a guest of the Animal Breeding Research Department, University of Edinburgh, where preliminary observations on embryonic mortality were made. Our thanks are due to Prôfessor F. A. E. Crew and the staff of the Animal Breeding Research Department for their hospitality and many kindnesses.

A HOMOZYGOUS FRIZZLE CHICK
Figure 4

The down is kept longer than usual, and after it wears off the chick remains nearly bare for the first year of life. At the close of the first year of adult life a more complete plumage appears (See Figure 2).

heterozygous (exhibition- and F_1-) Frizzle types. During their first year of life they usually are more or less bare over the whole body (Frontispiece *D* and *E*). The degree of bareness of such birds, however, is rather variable. Usually, there are only a few feathers on the head or none at all; the upper part of the neck shows some feathers, while the back is practically bare in most cases. As a rule some small feathers are found along the sternum, and the lower part of the thighs almost always is fairly well feathered. In the wings usually only the shafts of the primaries and secondaries are present and even these frequently are broken off at their base. There are no coverts or wing bow feathers. The tail feathers are either absent or only vestiges of their shafts are present. The skin of the bare parts, more particularly of head, neck, sacrum, and thighs usually shows an intense redness. Whatever feathers are present in such homozygous Frizzles, appear considerably narrower and are much more tightly curled than those of either one of the two other types. In the remaining parts of the body the definitive feathers fail to erupt. The down feathers are kept longer than usually, and only gradually wear off. After their loss the chicks appear bare (Fig. 4). At the time of the autumnal moult at the close of the first year of their adult life these birds usually develop a much more complete plumage consisting entirely of narrow and very curly feathers (Frontispiece *C* and Fig 2). At least one of Davenport's original four Frizzles undoubtedly was a homozygous female of this type (his Fig. 42, Plate 14). In exceptional cases homozygous birds may show such a plumage already in their first year (Fig. 3*C*). We obtained a pullet of this type from Mr. Paul Ives; she was a descendant of our English Frizzle stock. This more complete plumage of the two year old birds, however, soon after its appearance begins to be shed and worn off and after a short time the birds resume again the bare appearance which they had exhibited during their first year of life.

Microscopic Characteristics of Frizzle Feathers

A microscopic examination of feathers from neck, breast, back, and wing secondaries revealed structural changes corresponding to the degree of curling which the feathers exhibit in the different types of Frizzle fowls (Figure 3). The feathers of *F_1 Frizzles* (taken from crosses of Frizzles with Leghorns or with Rhode Island Reds) usually show only slight deviations from the normal structure (Figs. 5*B* and 6*E*). Apparently there is a greater tendency towards a lack of the barbules in the distal part of the barbs in the tip of the neck feathers and the hooklets show a less regular shape. The barbules of the breast feathers frequently bear straight bristles instead of hooklets. Similar conditions are found in the feathers of the back; in the latter it also was observed that the distal barbules occasionally are broader than

normal. In some instances both barbs and barbules show peculiar thickenings near the distal end of the barbs; the barbules frequently appear to be attached to the barbs and sometimes even to be fused with them. It seems as if in these places the outermost layer of the barbs and barbules had peeled off, possibly due to an imperfect keratinization, but still remained connected with its place of origin. In the secondaries of some of the birds the barbs are strikingly thicker than normal and show the equisetum-like structure typical for the fluffy part of normal feathers. The barbules are directed more towards the tip of the barbs and usually bear straight bristles instead of hooklets. In other instances the feathers are more normal but show a rather irregular arrangement of the barbules as if the latter were less stiff than normal and, thereby, had lost their typical arrangement. In many places the surface of the barbules seems to have worn off and the detritus fills the spaces between the barbules. It should be emphasized again, however, that on the whole the structural deviations of the feathers of F_1 Frizzles from normal ones are but slight.

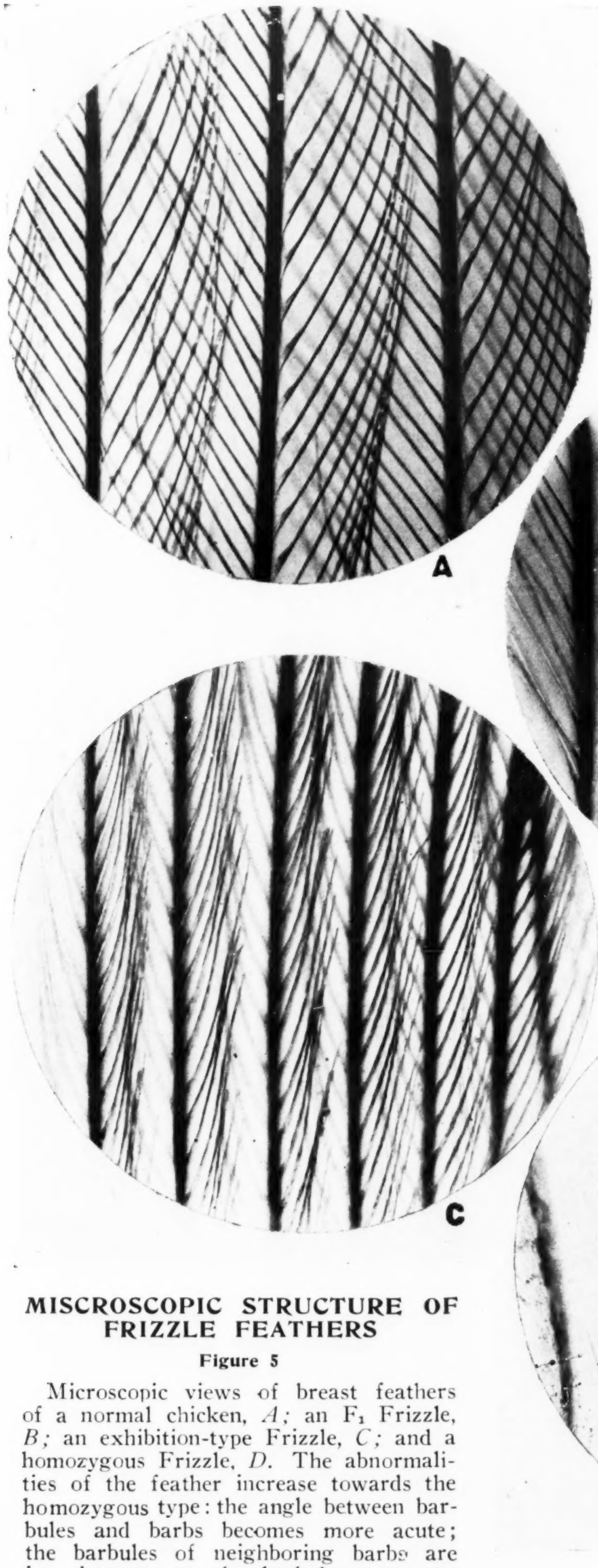
The feathers of *exhibition-type* (heterozygous) *Frizzles* show more conspicuous structural changes (Figs. 5*C* and 6*F*). The barbules of the neck feathers usually are strikingly thickened, and the distal ones are relatively short with blunt ends; the hooks frequently are missing altogether or are represented only by short and straight bristles. In feathers of the breast only the distal barbules and these only in certain instances were found to be thickened; the hooklets are present more regularly, usually as straight bristles. The direction of the barbules is strikingly abnormal: they form a more acute angle than normally with the general plane of the feather(the plane of the barbs with the rachis) and at the same time take their course more towards the tip of the barbs. The barbules for this reason are less well interwoven than in the normal feathers. In the feather tip the barbules frequently are missing at the distal end of the barbs. The abnormality in the direction of the barbules was also observed in feathers from the back. In these feathers the barbules usually are thicker than normal and bear no hooks and only rarely straight bristles.

In *homozygous Frizzles* the feather abnormalities are still much more pronounced than in exhibition-type Frizzles (Figs. 5*D* and 6*G*). This is particularly true for the direction of the barbules. These usually are closely attached to the barbs and, parallel to the barbs, directed towards the tip of the latter. The barbs themselves form a more acute angle with the rachis than normally, thereby being directed more towards the tip of the feather. The barbules of neighboring barbs are not interwoven. It can readily be understood how these structural changes produce feathers with a peculiarly narrow appearance. In feathers of the neck the barbules are longer than normal, and frequently have a very irregular outline with many waves and bends or even breaks. There are no hooklets. In breast feathers the distal end of the barbs in the feather tip shows very few or no barbules and the barbs themselves appear thickened. Similar conditions are found in feathers of the back. In secondaries all barbules are strikingly thickened, particularly in the distal part of the feather. Frequently they have a worn appearance. The barbules are segmented. In the distal part of the feathers most of the barbules have no hooklets; some show short straight bristles. In the proximal feather parts hooklets are found more regularly.

No definite macroscopic or microscopic differences could be established in the down feathers. Down of homozygous chicks, however, has not been examined.

Genetic Analysis

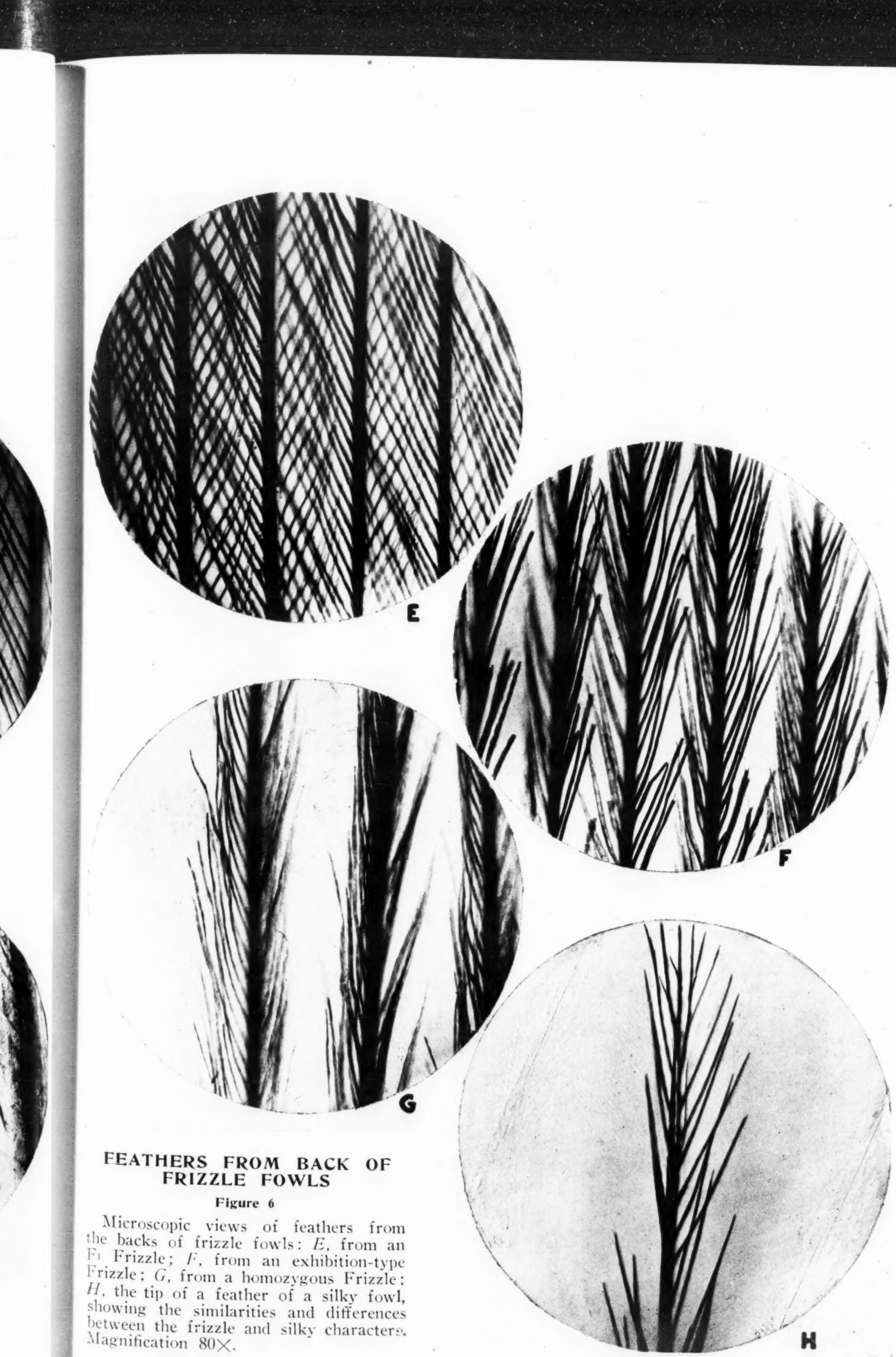
Our matings consisted of backcrosses of Frizzle by normal, crosses of heterozygous Frizzles *inter se,* and



MISCROSCOPIC STRUCTURE OF FRIZZLE FEATHERS

Figure 5

Microscopic views of breast feathers of a normal chicken, *A;* an F_1 Frizzle, *B;* an exhibition-type Frizzle, *C;* and a homozygous Frizzle, *D.* The abnormalities of the feather increase towards the homozygous type: the angle between barbules and barbs becomes more acute; the barbules of neighboring barbs are less interwoven, the barbules are more thickened and more defective. (The barbs are the larger parallel elements to which the barbules, the small interlacing branches, are attached. The barbs are branches of the main shaft, or rachis, of the feather.) Magnification 80×.



FEATHERS FROM BACK OF FRIZZLE FOWLS

Figure 6

Microscopic views of feathers from the backs of frizzle fowls: *E*, from an F_1 Frizzle; *F*, from an exhibition-type Frizzle; *G*, from a homozygous Frizzle; *H*, the tip of a feather of a silky fowl, showing the similarities and differences between the frizzle and silky characters. Magnification 80×.

genetic tests of birds supposed to be homozygous for frizzling by crossing them to Leghorns. These matings were designed to test the segregation ratios, to determine the nature of the extreme grade of frizzling (bare Frizzles), and to decide whether the Frizzle gene has a lethal action.

At hatching time Frizzle chicks cannot be distinguished macroscopically from normal ones. The age at appearance of the frizzled condition varies considerably, probably chiefly as a function of the general rate of feathering. In some chicks the frizzling is already definitely established two or three days after hatching, while others remain doubtful for as long as two weeks. The wing feathers exhibit the character earliest. It seems that temperature has some influence upon the time of first expression of frizzling since chicks hatched in summer or raised in heated batteries within a heated room tend to show the frizzled condition somewhat earlier than others. This may be due only to a general acceleration in the rate of feathering.

All Frizzle chickens used in the back-crosses were derived from a cross of Leghorn pullets by an American Frizzle cockerel. One mating consisted of American Frizzle pullets and a Bare-neck rooster with normal plumage. Out of 160 hatched chicks from this cross we obtained records for 135. The segregation among these chickens was as follows:

	Frizzle	*Normal*
Actual	62	73
Expected	67.5	67.5

Another back-cross consisted of American Frizzle pullets and a Leghorn cockerel. Out of 112 chicks hatched the nature of the plumage was recorded for 98, showing the following segregation:

	Frizzle	*Normal*
Actual	41	57
Expected	49	49

Finally, a back-cross was made between Leghorn pullets and an American Frizzle cockerel. In this experiment 95 out of 111 hatched chicks were recorded. These showed the following distribution:

	Frizzle	*Normal*
Actual	50	45
Expected	47.5	47.5

In all three back-crosses taken together we have records for 328 birds with the following segregation:

	Frizzle	*Normal*
Actual	153	175
Expected	164	164

These figures agree well with the expectation in back-crosses of birds heterozygous for one dominant factor. There is a slight excess of normal chickens. This is probably accounted for, at least in part, by chicks which died early and were recorded as normal when they actually would have developed into Frizzles.

A mating of heterozygous English Frizzles *inter se* yielded 108 chicks of which we have the records for 93. These were distributed in the different classes as follows:

	Frizzle		*Normal*
	Homozygous	*Heterozygous*	
Actual	23	50	20
Expected	23.25	46.50	23.25

The results agree very well with the expectation.

In two matings bare frizzles were tested for homozygosity by crosses with Leghorns. In one mating with three Frizzle females (two of American, one of English origin) 59 chicks were recorded: all Frizzles. The other mating consisted of Leghorn pullets and an American Frizzle male. In this cross 43 chicks were recorded, again all Frizzles. This is definite proof that the Frizzles which are more or less bare during the first year and have a very curly plumage later on, actually are the homozygous individuals.

In conclusion we may say that our breeding experiments demonstrate that frizzled and normal plumage are determined by a single factor pair, the frizzled condition being dominant over the normal plumage, that the Frizzle gene has no recessive lethal action but

that homozygous Frizzles exhibit a pronounced decrease in viability.

Incubation Data

We have to examine next the records of embryonic mortality and hatchability in our different Frizzle crosses. In Table I are given the actual and percentage figures of embryos which died during the different periods of incubation and of chicks which hatched in the various Frizzle crosses made in 1929. The Frizzle pullets in the crosses of heterozygous American Frizzles by a Bare-neck rooster and by a Leghorn cockerel, and the Frizzle cockerel mated to Leghorn pullets all were F_1 hybrids from a cross of Leghorns and American Frizzles. They showed the plumage typical for such F_1 birds. In these crosses the embryonic mortality was low and the hatchability was high (69-82%). In our mating of English Frizzles *inter se* two different groups of pullets were bred to a heterozygous exhibition-type Frizzle cockerel. The first group consisted of F_1 Frizzle pullets derived from a cross of normal Rhode Island Red females and the Frizzle rooster imported from England, while the second group was made up of exhibition-type Frizzle pullets which had imported Frizzle stock for both parents. The eggs of the first group (F_1 birds) showed a low embryonic mortality and a good hatchability (68%), while in the second group (exhibition-type) the embryonic mortality was much higher and the hatchability correspondingly lower (45%). Finally, the crosses of homozygous Frizzles and Leghorns show a low embryonic mortality and high hatchability (75%) where normal pullets are mated to a homozygous Frizzle male, while in the reciprocal cross the embryonic mortality was high and the hatchability low (43%).

Are these differences in embryonic mortality significant? All birds in our cross of exhibition-type Frizzles *inter se* were descendants of the Frizzle females and the one Frizzle male purchased in England, and since in the process of selection the breeder of this strain probably had to inbreed to a certain degree, it could well be that the low hatchability in our mating of the progeny of these birds was due to inbreeding rather than to pecularities of the Frizzle stock. The homozygous Frizzle females, on the other hand, were crossed to a Leghorn cockerel, and there can be little doubt that the poor hatchability in this cross significantly differs from the good hatches in back-crosses of F_1 Frizzle pullets, in crosses of F_1 Frizzle pullets to an exhibition-type Frizzle male, and in the cross of a homozygous Frizzle male to Leghorn pullets.

To check the significance of these results, we have collected new data in 1930, and these are presented at the end of Table I. One mating consisted of exhibition-type Frizzles *inter se*. Eight pullets were involved in this cross. The hatchability varied from 29 to 53% with an average of 38.2%. These birds are the F_2 generation of a cross of the original English Frizzle male to unrelated Rhode Island Red pullets. Although this constituted a half-brother-sister mating the degree of inbreeding is not sufficient to explain the low hatchability in this cross. Our second mating consisted in a cross of four Leghorn pullets to an English exhibition-type Frizzle cockerel. In this cross the hatchability ranged from 51 to 74% with an average of 61.4%. The same exhibition-type male was bred to three homozygous Frizzle females (two American, one English). In this mating the hatchability ranged from zero to 47% with an average of 19.2%.

The fact that exhibition-type Frizzles extracted from an out-cross to Rhode Island Red stock gave a similarly lower hatchability than the direct descendants of the original English Frizzles seems to show that inbreeding was not responsible for the low hatchability in these crosses. The mating of homozygous Frizzle females to an exhibi-

tion-type Frizzle male also gave a very low hatchability even though two of the three females used in this experiment were entirely unrelated to the male. A cross of an exhibition-type male to Leghorn pullets, on the other hand, yielded normal hatchability.

In general, we may say that the incubation data for 1930 are in good agreement with those obtained in 1929, and taken together they seem to justify the following general conclusion: The embryonic mortality and hatchability in Frizzle crosses is normal if F_1 Frizzle females are mated to a Frizzle or to a normal male, or if normal females are mated to a Frizzle male of any one of the three different types (F_1, exhibition-type, and homozygous). The embryonic mortality is high and the hatchability low if the Frizzle females are of exhibition stock or homozygous, even if they are crossed to a male with normal plumage.

Discussion

Plumage characteristics comparable to those of the Frizzle fowl are known in pigeons, geese, and canaries. According to the descriptions by Lyell, Fulton, Dürigen and others, it appears that in the Frizzled or Frillback pigeon the peculiarity typical for this breed does not always extend over the whole body but may be confined to certain areas. Similar variations seem to exist in different strains of frizzled canaries (Noorduijn), and according to Tegetmeier and Dürigen also in Sebastopol geese. It appears that in chickens usually the entire plumage is involved but Tegetmeier mentions Frizzle fowls with frizzled hackles only which he had seen in Darwin's collection.

No detailed descriptions seem to exist for the feathers of frizzled pigeons, canaries or geese. Fulton states that the feathers of Frillback pigeons are longer and more pliable than those of normal individuals. In Sebastopol geese Tegetmeier described an extreme elongation of the feathers of the back (scapulars and tail coverts); these feathers are bifurcated near the base and twisted. The secondaries and tail feathers are also elongated, although to a less extreme extent, and twisted. In addition the feathers of the head, upper neck, breast, and thighs may be frizzled (Dürigen). An elongation of feathers has not been observed in Frizzle fowls; no exact comparative measurements, however, have been made.

Our microscopic observations have shown that the chief characteristics of the feathers of Frizzle fowls consist in an absence or modification of the hooklets, a thickening of the barbules and barbs, and alterations in the direction of the barbules and barbs. The distal parts of the feathers appear to be more modified than the proximal ones. In the Silky fowl, on the other hand, the modifications of the feathers consist chiefly in an absence of the hooklets, an elongation of the barbs, frequent bifurcations of the barbs, and an irregular position of the barbules. Punnett states that "in the long feathers of the wing it is only towards the end of the feather that the hooklets are not formed. . . . ." A comparison of the findings in Frizzle and Silky feathers shows that one of the principal characteristics in both is the lack (or modification) of hooklets; in both the distal parts of the feather appear more abnormal than the proximal ones; bifurcations seem to occur in Frizzle feathers in rare instances, and the angle between the barbules and barbs in both tends to be smaller than normal (Fig. 6*H*). From the incomplete reports which are available it would seem that the plumage of the Sebastopol goose occupies an intermediate position between Silkies and Frizzles.*

Earlier observers have already recorded that the general constitution of Frizzle fowls is weaker than that of other breeds. Thus, Tegetmeier quotes Hewitt as saying: "They [the Frizzles]

*A comparative and embryological study of the different types of frizzling is planned.

usually are of a somewhat sickly appearance, and generally, if handled feel thin and spare. . . . . the fowls often became diseased, and were generally out of condition, although enjoying the same advantages as all the other varieties that remained in perfect health. They are quickly prevented from laying by the occurrence of severe weather, at which time they look very forlorn and wretched; and always appear to suffer far more from exposure to cold and wet than the generality of fowls." Tegetmeier himself adds to this report that he has not "quite so unfavorable" an opinion of their merits, possibly because living in a dryer locality. In our own experience, first crosses of Frizzles (F_1 birds) need little more care and attention than non-frizzled chickens and the females may be quite good layers; exhibition-type Frizzles demand a higher measure of protection from adverse environmental conditions and the females are less reliable layers. Homozygous Frizzle fowls, due to the extreme deficiency in their body covering, are very difficult to raise. Most of them become victims to colds and die during growth. Although we took such chicks off the range as soon as they were recognized as homozygous individuals, we have succeeded in raising only a relatively small number of them, and in spite of the fact that these animals were permanently kept with brooder stoves, few survived their first year of adult life. Furthermore, most of the homozygous individuals which survived beyond the growing period remained sexually immature during the remainder of their life. This holds equally true for males and females.* Among those which became mature, however, we have had two or three good layers and a very fertile cockerel.

We have already seen that there were between our different matings definite differences with regard to embryonic mortality and hatchability. The fact that the embryonic mortality is high in eggs from heterozygous exhibition-type and from homozygous Frizzle females whether they are mated to frizzled or to normal males, while even homozygous Frizzle males apparently have no detrimental influence upon embryonic development if crossed to normal females, indicates that this situation is not determined by *genetic* peculiarities of the Frizzle fowl.

An explanation is suggested by observations which Benedict has made on "scraggly" pigeons from Riddle's stock ("scraggly" in pigeons is a character as yet undescribed similar to frizzling in the fowl). He found that in such animals the basal metabolism is increased about 50% as compared with normal pigeons. It seems likely that a similar situation prevails in Frizzle fowls.† It seems probable that the degree of plumage deficiency is chiefly responsible for the amount of extra loss of body heat which in turn creates a corresponding increase in basal metabolism. If this is true, we should expect the F_1 Frizzles with their low expression of the frizzled condition to be much more normal with regard to the basal metabolism than exhibition-type Frizzles and that homozygous Frizzles will show a still higher basal metabolism than exhibition-type birds. This assumption is supported by our observation that the food consumption of exhibition-type and homozygous Frizzles is considerably higher than that of normal chickens.

Scraggly pigeons, according to Benedict, are always sterile. Similarly, a high percentage of the homozygous Frizzle chickens of both sexes remains permanently immature. It seems likely that in both instances the greater loss of body heat with its consequent increase in basal metabolism depletes the organism of its resources to such a

*A report concerning the histo-pathology of the gonads of such animals will be published elsewhere.

†Determinations of the basal metabolism will be made.

degree that it always or frequently becomes impossible for the gonads to differentiate to a functional condition.

A small percentage of the homozygous Frizzle fowls, however, and all the exhibition-type Frizzles reach sexual maturity. Our observations concerning embryonic mortality and hatchability in the different crosses of such birds can all be understood if we assume that the greater increase in basal metabolism in the homozygous and exhibition-type Frizzles, as compared with F_1-Frizzles, interferes with the production of normal eggs but does not interfere with the production of normal sperm. Since the eggs contain all the storage material for the development of the embryos it seems likely that deficiencies should occur in the eggs rather than in the sperm. The fact that frizzled canaries (according to a personal communication from Dr. H. Duncker) are known to be "poor breeders" may be taken as a further indication that these reproductive disorders are a direct physiological (metabolic) effect of the frizzled condition.

Summary

Our experiments with Frizzle fowl of English and American origin lead us to the following conclusions:

1. The difference between frizzled and non-frizzled plumage is determined by a single factor pair. Frizzling is dominant.

2. The gene for frizzling has no recessive lethal action.

3. Frizzle fowls bred for exhibition purposes generally are heterozygous.

4. Frizzled chickens from crosses of frizzled and non-frizzled birds (F_1 Frizzles) exhibit a much lower degree of frizzling than exhibition-type Frizzles.

5. Homozygous Frizzles are almost bare during their first year of life. At the time of the autumnal moult at the close of the first year of adult life homozygous Frizzles acquire a plumage with a much higher degree of frizzling than that shown by exhibition-type Frizzles. The feathers are narrow and curled. This new plumage is shed and worn off again soon after it has grown out.

6. Microscopically, the feathers of F_1, exhibition-type, and homozygous Frizzles show distinct differences. In F_1 birds the deviations from normal conditions are slight. In feathers of exhibition-type Frizzles part of the barbules are thickened; in some places the hooks are missing entirely, in others they have the shape of straight bristles; the barbules form a more acute angle with the general plane of the feather; in feathers of the breast the barbules are frequently missing in the tip of the feather. Feathers of homozygous Frizzles show still more extreme structural abnormalities. The barbules usually are closely attached to the barbs; the barbs themselves form a smaller angle with the rachis than normally. The barbules of neighboring barbs are not interwoven. In other respects the changes in the structure of the feathers are similar to but more extreme than those in exhibition-type Frizzles. Barbules and barbs frequently have a worn appearance.

7. Embryonic mortality and hatchability in Frizzle crosses are normal if F_1 Fizzle females are mated to a Frizzle or a normal male, or if normal females are mated to a Frizzle male of any one of the three different types. The embryonic mortality is high and the hatchability low if exhibition-type or homozygous females are used, even if they are bred to a male with normal plumage.

8. A high percentage of homozygous Frizzles of both sexes never reaches sexual maturity.

9. The higher the degree of frizzling the more susceptible are the birds to adverse environmental conditions.

10. As a working hypothesis it is assumed that, analogous to the conditions in scraggly pigeons, the basal metabolism is increased in Frizzle fowls. It seems likely that the increasing plumage deficiencies in F_1, exhibition-type, and homozygous Frizzles are

associated with a similar increase in basal metabolism. The high rate of embryonic mortality in eggs from exhibition-type and homozygous Frizzle females is explained by deficiencies in the storage material of the eggs due to the increased basal metabolism of the mothers. Spermatogenesis appears to be normal whenever males reach maturity. The high percentage of sterility among homozygous Frizzles is also accounted for by the increase in basal metabolism.

Author's Postscript: A paper by F. B. Hutt (The genetics of the fowl. I. The inheritance of frizzled plumage. *Journal of Genetics*, vol. 22, 1930) covering the same field has been published since this report was prepared for publication.

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TABLE I—Frizzle Matings—Embryonic Mortality and Hatchability—1929 and 1930

Mating	No. of fertile eggs.	Actual Embryonic mortality				Hatched	Percent Embryonic mortality				Hatchability
		1-6	7-14	14-16	17-22		1-6	7-14	14-16	17-22	
1929											
Heterozygous Amer. Frizzle♀♀ [F_1(Leghorn x Frizzle)] x Leghorn♂	159	13	7	0	26	113	8.18	4.4	0	16.36	71.07
Heterozygous Amer. Frizzle♀♀ [F_1(Leghorn x Frizzle)] x Bare neck♂	206	17	3	0	17	169	8.25	1.45	0	8.25	82.04
Leghorn♀♀ x Heterozyg. Amer. Frizzle♂ [F_1(Leghorn x Frizzle)]	172	14	4	0	36	118	8.14	2.33	0	20.93	68.6
Heterozygous English Frizzle♀♀ [F_1(Rhode Island Red x English Frizzle)] x English exhibition-type Frizzle♂	94	1	4	2	23	64	1.06	4.26	2.13	24.47	68.08
English exhibition-type Frizzles inter se	96	9	6	1	37	43	9.38	6.25	1.04	38.54	44.79
Homozygous Frizzle♀♀ x Leghorn♂	213	36	14	3	69	91	16.9	6.57	1.41	32.3	42.7
Leghorn♀♀ x Homozygous Amer. Frizzle♂	77	3	2	1	13	58	3.9	2.6	1.3	16.88	75.32
1930			7-16					7-16			
English exhibition-type Frizzles inter se	191	20	20		76	73	10.5	10.5		40.8	38.22
Leghorn♀♀ x English exhibition-type Frizzle♂	140	9	6		39	86	6.4	4.3		27.9	61.4
Homozygous English and American Frizzle♀♀ x English exhibition-type Frizzle♂	52	4	2		36	10	7.7	3.9		69.2	19.2

HOW FARM ANIMALS INHERIT

A Review

THIS book* will stand high in the list of attempts to make modern genetics understandable and useful to the practical animal breeder. Whether after all a detailed understanding of technical genetics is necessary or even very useful to the commercial animal breeder is another question. Probably it is a mental relief to the breeder to understand why the things occurred which he has seen in his herd, but one may read this book and still be a little skeptical of the *necessity* of informing stockbreeders about chromosomes, crossing-over, phenotype, heterozygote, and some of the other technical terms of modern genetics. "Heredity in Live Stock" is one of the least technical among the many books in this field. For example, the reviewer did not notice a single use of the much over-worked "germ plasm." Yet it seems likely that some further freedom from technicality could be attained, especially in the first three chapters, with an increase in the readability of the book and with at least no decrease in its utility to the stockman not already acquainted with genetics.

The first three chapters introduce and treat the subject of Mendelism, the mechanism of inheritance and linkage. The distinction is not drawn very clearly between "factors" and "characters." Other than this, criticisms of the first three chapters concern matters of personal opinion, such as whether the symbolism used for illustrating linkage on page 26 is as easily understandable as other possible illustrations would have been.

Chapters four and five are devoted to the inheritance of size. It is only in these chapters and the two following ones which treat of the inheritance of milk and fat production that the professional geneticist will find much to criticize in the subject matter. The criticisms here will be directed almost entirely toward the author's attempt to interpret many quantitative differences as caused by differences in one or two factors. Wriedt's views as to the usual simplicity of the genetic basis for differences in quantitative characters as expressed in this book are quite in accord with the views expressed even in his last articles on inheritance in dairy cattle. Those views are rather contradictory to the views of most geneticists, especially of those who have worked with highly inbred material which has been purified to the point where even the smaller genetic differences in quantitative characters could be manifested.

Inbreeding

Four chapters are devoted specifically to inbreeding. The treatment, while failing to emphasize many of the general consequences of inbreeding, yet is very readable and throughout carries the conviction that the man who wrote it knew farm animals and the general practice of animal breeders intimately. It should be excellent for introducing practical animal breeders to the modern genetic interpretation of inbreeding and, on account of the author's evident sympathy for and familiarity with the problems of the practical animal breeder, this treatment of the subject as an introduction is apt to carry conviction. Incompleteness is the only serious fault which the professional geneticist will find with the discussion of inbreeding.

The author's interest in lethal factors makes it not at all surprising that this subject receives considerable detailed mention and that many of the illustrations deal with lethals, especially in the discussions of inbreeding and also in

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*Heredity in Live Stock, by the late CHRISTIAN WRIEDT, Minister of Agriculture, Norway. Pp. 179. 18 Chapters. 70 Illustrations. Price, $3.00. Macmillan & Co., London. 1930.

the very interesting chapter on "Great Sires and Lethal Factors."

Probably the high point of the book is reached in the chapter on "Fairs and Fancy Points" and in the chapter on the real significance of pure breeds in Animal Husbandry. The chapter on the valuation of pedigrees, while emphasizing some of the common fallacies on this subject, yet falls short of pointing out many of the constructive uses which can be made of pedigrees. The chapters on superstition and on the inheritance of acquired characters are quite readable but have probably been equalled in many other books. Certainly many others have treated those subjects in greater detail.

Physiology and Sex-Determination

It is refreshing to find a book on Animal Breeding which devotes so little attention to the physiology and mechanics of reproduction as this one does, since most practical animal breeders can do little or nothing to change or control those processes but must work the improvements for which they hope through the selection of sires, like or unlike their females in certain respects of pedigree or progeny tests or individuality. The references to the subject of sex-determination are also refreshing in their brevity although some question might be raised as to the wisdom of drawing illustrations on sex-determination only from poultry without stating that the mechanism of sex-determination is reversed in mammals. As justification for this, there is of course the fact that only the breeders of poultry have yet been able to utilize the mechanism of sex-determination to commercial advantage.

Not the least attractive among the features of the book is the wealth of illustrations of inbreeding or of other breeding practices drawn from breeds and localities unfamiliar to most American students of animal breeding. The history of the Kladrub horse stud in Bohemia, of the Frederiksborg stud in Denmark, and of the Tofe horses which form the basis of the present Norwegian East-Country horse are especially interesting examples of this. One learns with considerable surprise that 45 per cent of the bulls registered during the years 1910-20 in the herdbooks of the Norwegian Telemark breed of dairy cattle had sires that were six years old or older. This is in marked contrast to the few investigations yet made of the age of dairy sires in America and gives encouragement to those who think something worthwhile may be accomplished by campaigns for the use of proved sires in dairy cattle and for the saving of sons from none but the older and well-proved sires. Some may catch their breath at the author's recommendation that all sires be tested by breeding them to at least twenty of their own daughters as soon as possible, in order to make sure whether they carry any lethal or other undesirable recessive factors and to determine whether they are good enough that one would care to save their sons for breeding purposes. Yet after all, is there anything wrong in principle with this suggestion? And would there be any practical difficulty to overcome other than widespread reluctance of most breeders to undertake such close inbreeding?

The general public will find this book readable and interesting. The professional geneticist will find little to criticize in subject matter other than the extreme emphasis on the fewness of the factors concerned in the inheritance of quantitative characters. Another matter for some regret is the scanty treatment accorded to general consequences expected from various systems of selection, inbreeding, and crossbreeding as actually practiced by animal breeders. The new subject matter in the book is scarce except on the subject of the effects of shows and fairs and other methods for standardization of livestock and how those measures actually work out in practice. Many of these things and of the illustrations will be new to geneticists not acquainted with the problems of prac-

tical animal breeding. The book will interpret to the animal breeder unfamiliar with genetics many of the facts which he has known for a long time but for which he has not known the reasons. Many of these facts are very neatly explained here as a natural consequence of the principles of modern genetics.

JAY L. LUSH.

Lamarck

IT is a curious irony that the name of Lamarck has become attached only to a minor phase of his researches and speculations. The discrediting of these has tended to make us forget the great contributions this versatile man made to many departments of biology, and to cause us to overlook the remarkable example his life was of a scientific genius who performed great labors in the face of tremendous obstacles. As the author of *Flore Francaise* he has been called the French Linné, and his *Animaux sans Vertèbres* ranks him among the greatest zoologists of his time. Taken out of their context some of his statements regarding the inheritance of acquired characters lend themselves to the burlesque which is frequently made of his views of evolution. Taken as part of the whole they do not seriously detract from the general view. In spite of references to Lamarck's views as "veritable rubbish," Darwin admitted that "the conclusions I am led to are not widely different from his; though the means of change are wholly so." Probably as good a general statement of Lamarck's views as any he made is the following, delivered in 1800 in a lecture, and later (1801) appearing in the preface to *Animaux sans Vertèbres:*

> It appears, as I have already said, that *time* and *favorable conditions* are the two principal means which nature has employed in giving existence to all her productions. We know that for her time has no limit, and that consequently she has it always at her disposal.
>
> As to the circumstances of which she has had need and of which she makes use every day in order to cause her productions to vary, we can say that they are in a manner inexhaustible.

That Lamarck picked out some of the wrong circumstances in elaborating his theory is not surprising—even natural selection as a cause of variation is not without objections. He must be credited with keen insight in realizing that a connection existed between relatively endless time and varied circumstances in producing the amazing array of living organism, which in form and in degree of complexity he conceived as constituting a graded, related series varying from the simplest to the most complex. His views as to relatively endless time are clearly stated and when Cuvier attacked his theory of evolution by calling attention to the striking similarity between mummified Egyptian cats and their modern descendants, Lamarck expressed the opinion that two or three thousand years was an entirely inadequate period to produce any marked change. Some of his views are strangely reminiscent of the "modern" concept of relativity.

Lamarck, whose full name was Jean Baptiste Pierre Antoine de Monet, Chevalier de Lamarck, was the youngest of eleven children. He was born August 1, 1744, at Bazentin-le-Petit, a little village in Picardy, between Albert and Bapaume. The family came originally from Southern France, and had among its members a number who were modestly distinguished in their chosen profession of arms. Reluctantly destined for the priesthood, Lamarck reverted to a military career on the death of his father in 1760,

(*Continued on page* 336)

TEMPERATURE EFFECTS ON THE COLOR OF THE SIAMESE CAT

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THE investigation of the process of inheritance only by means of formal breeding analysis is not a sufficient study of the problem. Thus it is a well known fact that the colors of animals are heritable characters. However, the genetic factors determining pigmentation can produce it only under strictly fixed external conditions. The investigation of the mechanics of development of pigmentation permits us to state how the genes produce their effects, and how the realization of the character takes place.

The pattern of the Siamese cat provides excellent material for the study of the realization of the pigmentation. The body-color of the pure bred individual is light cream, fawn, or chocolate without any body-markings. Face, ears, feet, and tail—i. e., the so called points—are clearly defined, dark brown (almost black). (Figure 7.) The eyes are opalescent blue with milky grey shade. The pupil reflects a ruby light which shows the small amount of pigment in the iris.* This pattern is very similar to that of the Himalayan rabbit with the exception of the body color which in the latter is pure white. Another difference is that the eyes of the Himalayan rabbit are absolutely devoid of pigment—therefore pink. Bateson[2] and Castle[3] have pointed out this similarity, and Castle noticed that it perhaps extends to the mode of inheritance; viz. both patterns are recessive to the self color and can carry as cryptomeres specific pigment factors (for instance that of the dominant chocolate black color).[13] It is difficult to compare in details the genotypical constitution of both animals because of our insufficient knowledge of the Siamese cat.

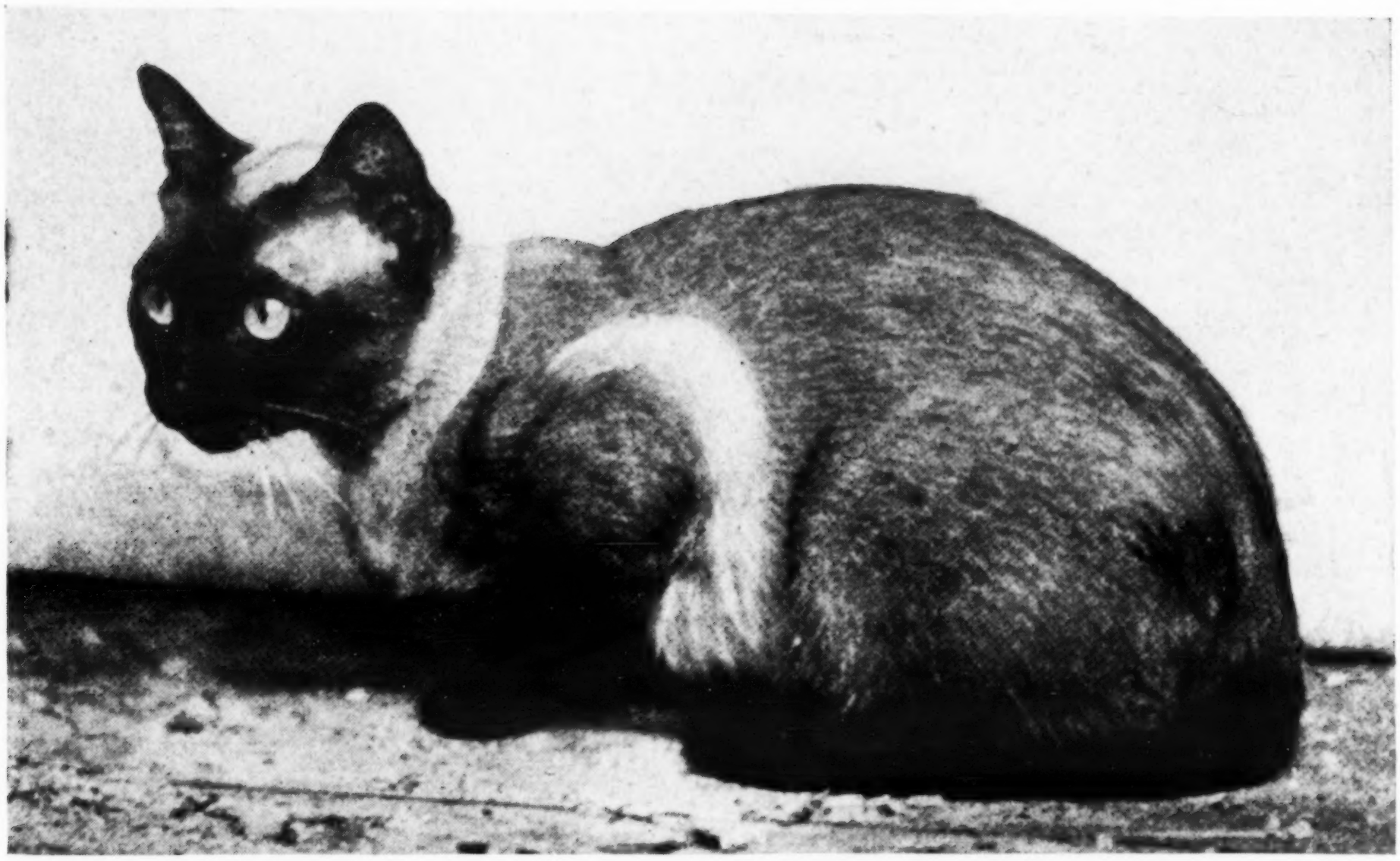
Color Changes In Relation to Temperature

W. Schultz[11] showed that the pattern of the Himalayan rabbit can be changed under the influence of cold, and one of the present authors studied the temperature at which the change of the color takes place.[5, 7] Naturally the idea came to the authors to investigate the question: is there any similarity between the temperature reaction and the mode of inheritable realization in the Siamese cat and the Himalayan rabbit as well as in their phenotypes and the mode of inheritance? To solve this problem a pair of pure bred Siamese cats was imported to Moscow from Germany. Just after their arrival on July 15, 1927 they were placed in a wooden building with comparatively low temperature which varied from — 3°C to + 16° and never was higher than + 19°C.

When the time of the autumn moult came, the cats were in conditions of temperature lower than that of an ordinary room whereas usually they are kept as pets with great care on warm cushions.

During the moult the color and the pattern of these cats gradually but *continually* changed. On their arrival from Germany their bodies were of a dark cream color, their bellies were slightly colored (pale cream) and the points were well defined. After two and a half months, i. e., by October 1, 1927, the color had become considerably darker and later the newly grown hair on the side and back became much

*See Iljin, N. A., The Ruby Eye in Mammals. *Trans. Lab. Exp. Biol.* Zoological Park of Moscow.



THE NORMAL SIAMESE CAT

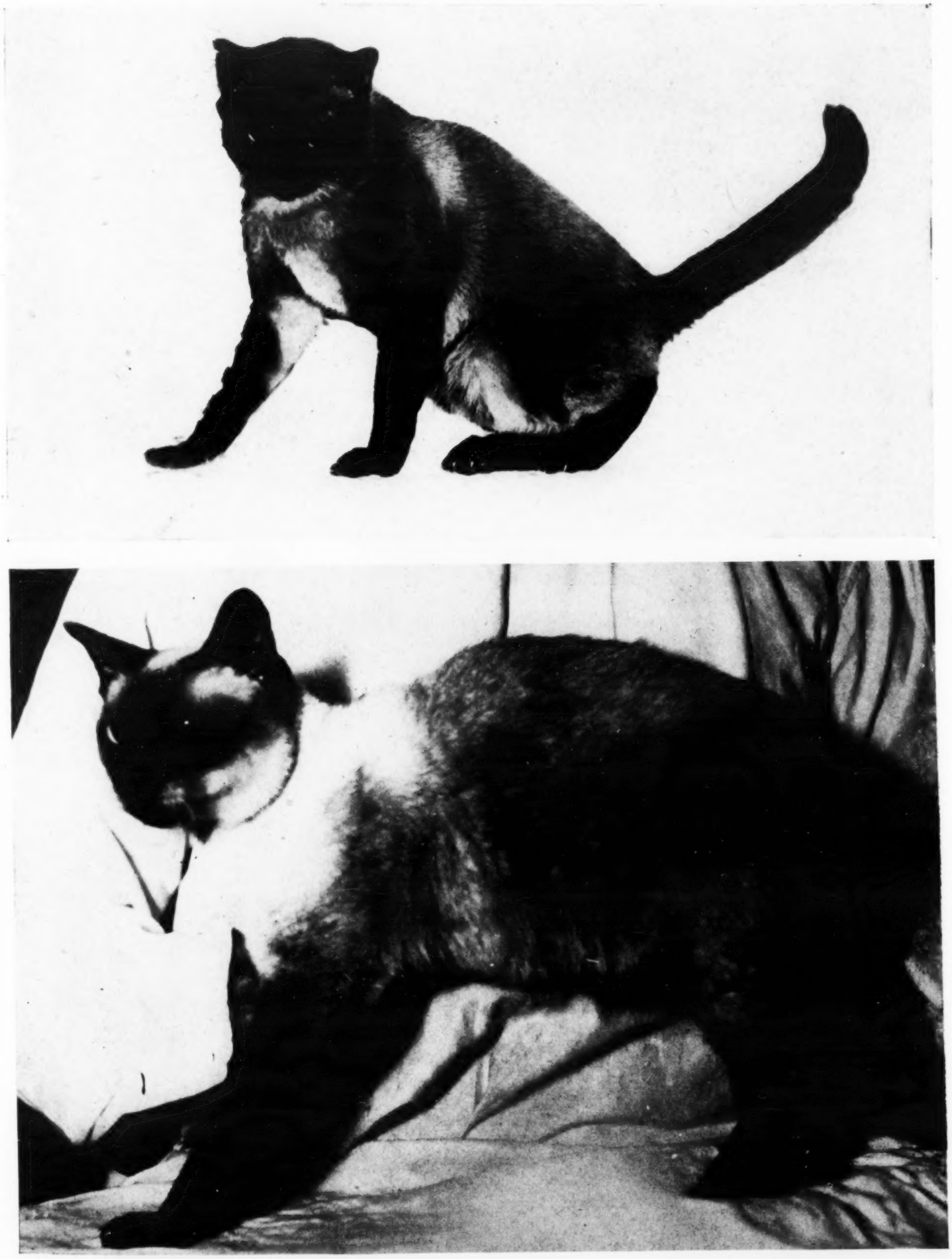
Figure 7

The Siamese cat under normal conditions as a house pet has a light cream or fawn body color, with dark brown "points," (face, ears, feet, and tail). The pupil reflects ruby light. The distribution of pigment in the pelage has been found to be controlled by temperature, the lower the temperature the darker the coat. (See Figure 8).

darker, i. e., light fawn or chocolate. By December 15 the change of color was mostly accomplished. The body was chocolate, the points became more intensively pigmented and even, so to say, a new point appeared on the shoulder and on the sides of the croup in the form of an irregular horse-shoe of a dark chocolate color. These changes of color must be considered as a result of the influence of low temperature. The formation of the dark spot on the shoulders is a result of a greater heat-loss of this body-part lying on bones of the shoulder girdle.

To determine definitely that the intensified pigmentation was the result of the influence of low external temperature it was necessary to show that the high temperature gives an opposite effect. To test this point the following experiments were made:

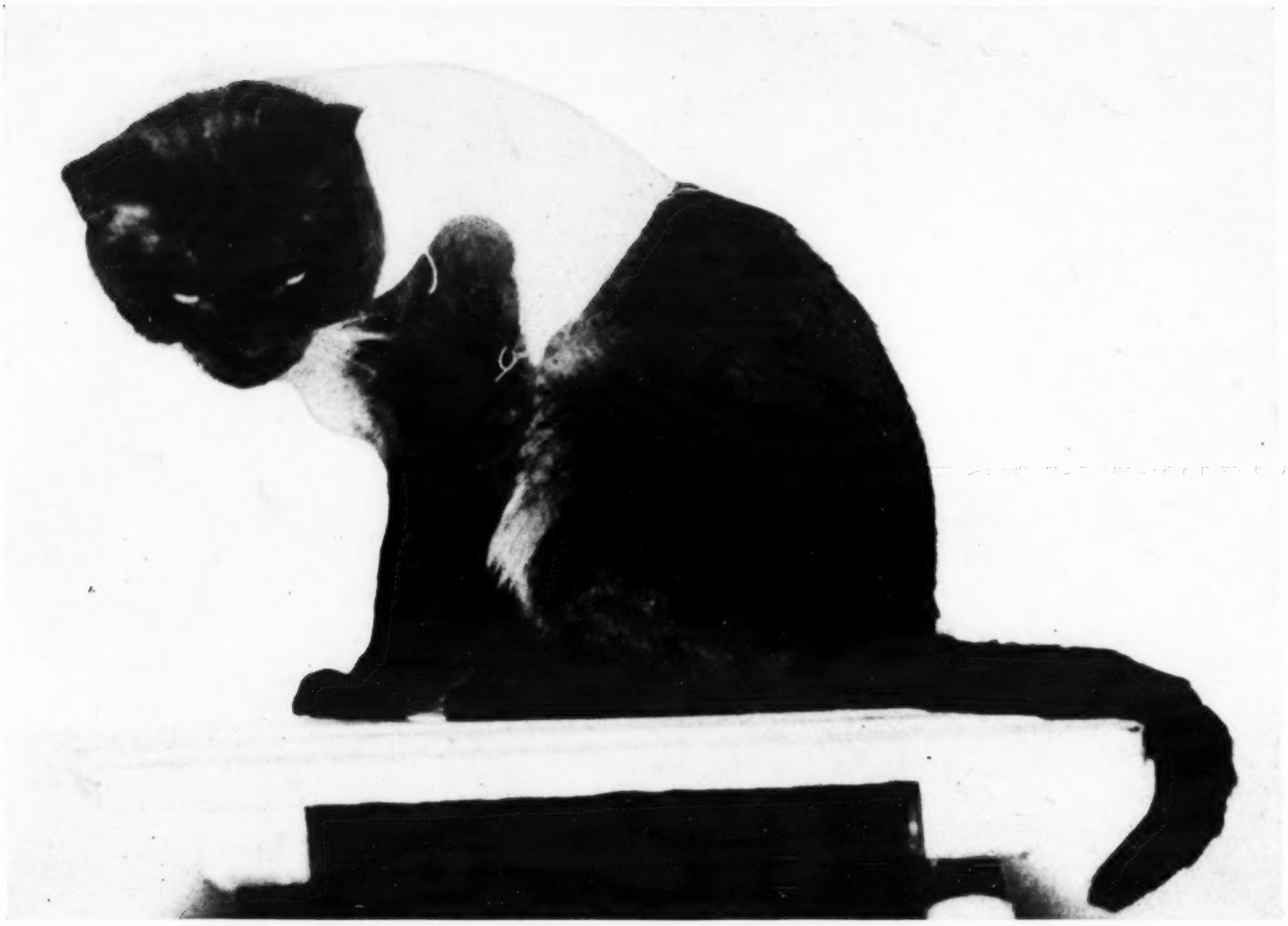
On October 7, 1928, a certain amount of the newly grown dark-chocolate hair of the chocolate black shoulder spot was removed and a bald place about 4 cm. in diameter was obtained. Wadding was laid on the skin, a cotton bandage was put on it and all this was tied to the shoulders. The layer of wadding reduced the heat-loss and under the bandage a temperature from + 34.5°C to + 36°C was established. On October 30 the bald spot had begun to cover with hair and three weeks later the bandage was taken off. All the bald place was covered with hair and was clearly marked as a light spot on the black shoulder "point". The greater part of the newly grown hair had chocolate tips and purely white pigmentless base. Besides this there was a considerable amount of entirely colorless hair, having no pigment either in cortex or in medulla. The repetition of this experiment gave identical results. Thus it is clear that at a low temperature the intensely pig-



LOW TEMPERATURE COLOR REACTION OF THE SIAMESE CAT

Figure 8

(Above) Male Siamese cat with dark colored pelage produced instead of the "normal" coat color as a reaction to lowered temperature. The "points" are so dark brown they are almost black, and the body color is chocolate. A new "point" has appeared on the shoulder, due to the greater heat loss over the shoulder girdle. (Below) Female Siamese cat, with dark-colored pelage produced under the influence of lowered temperature.



BANDAGED TO INCREASE THE TEMPERATURE

Figure 9

Siamese cat with the cotton bandage for warming the shoulders. The hair had been shaved from an area under the bandages, and the new hair contained much less pigment.

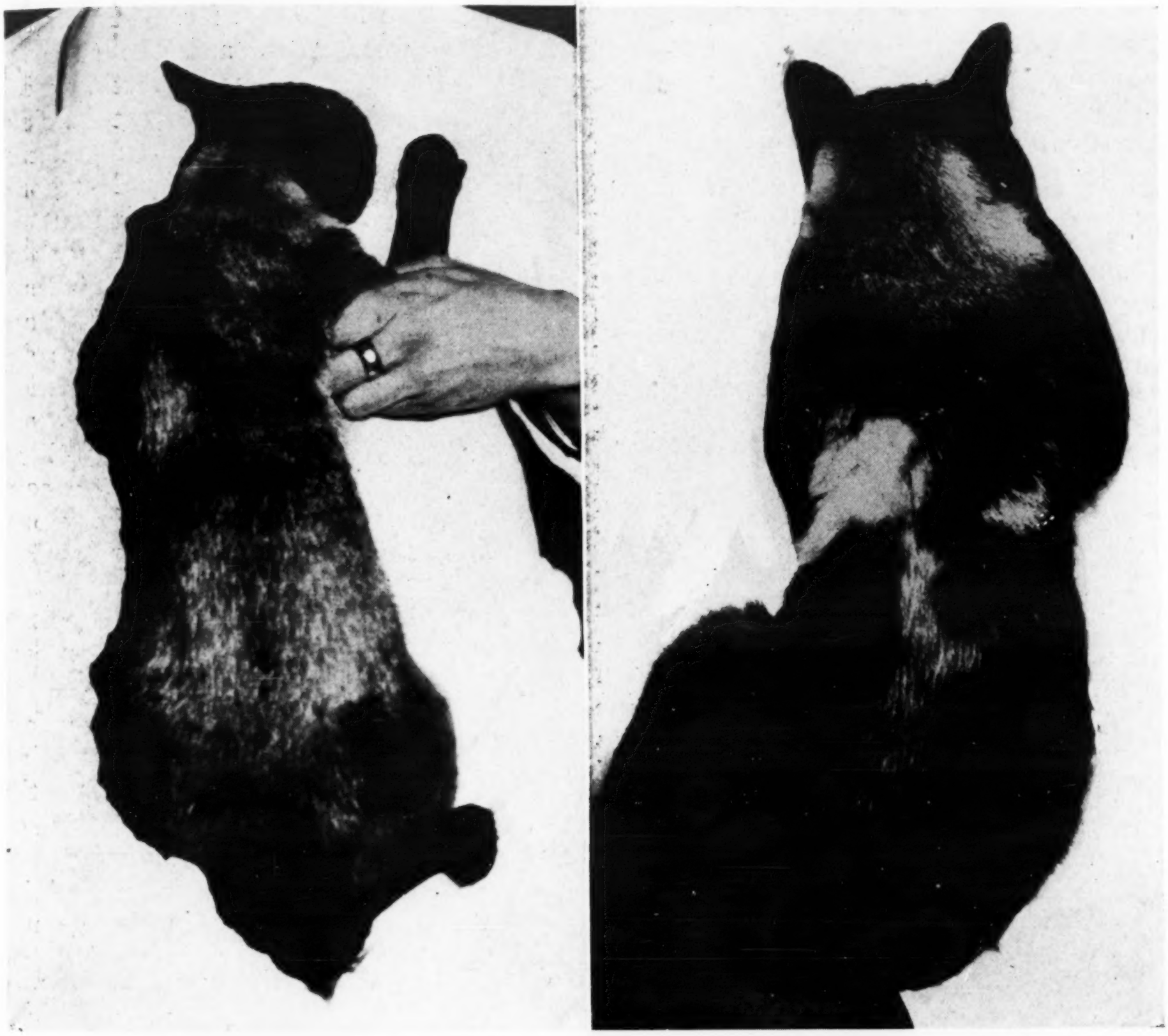
mented hair grows whilst at higher temperature it is slightly pigmented, nearly white.

Among the light colored hair there is a certain amount of "banded" hair: viz—chocolate tip, light cream subapical band and white base. It is clear that when the bandage was put on, these hairs had already begun to grow in relatively low room-temperature—therefore the pigment production was normal—and the pigmentless base grew at higher temperature.

Taking off the warming bandage some time afterwards allowed again the influence of the low room temperature and thus once more determined the appearance of pigmented hair. A month after taking the bandage off, among the white hair grown on this place some dark pigmented hair appeared. By the end of January, 1929, the pigmented hair had grown through the white spot to such an extent that it had become only slightly marked on the dark chocolate-black shoulder point.

A similar experiment on the female gave the same result with the exception that the color of the female remained on the whole considerably lighter than that of the male.

After this experiment, attempts were made to grow white hair on the ears and on the fore foot. As the warming bandage could not give the desired result it was decided to induce a local hyperaemia of the ear and thus to obtain a considerable increase in its temperature.[8, 9] As the agent to produce hyperaemia absolute xylol was used. It was applied as a periodical wetting of the ear. The first experiments of



WHITE SPOTS OF NEW HAIR

Figure 10

The white spots on the shoulders and on the back of Siamese cats produced by a local increase of temperature under the warming bandage.

short continued xylolisation (3 times with intervals of 3—4 days between the wettings) gave no effect. The pigmentation of the grown hair was not changed. A more continual treatment by xylol (9 times for the male with intervals of 1—3 days and 10 times for the female with the same intervals) and as a result a more continual hyperaemia gave the wanted effect: the growth of the pigmented hair with white tips and even of occasional *pure white,* pigmentless hair. The same result was obtained on the fore foot. The nasal point and the tail were not exposed to such a treatment because of the difficulty of working with these points.

Thus the warming of points by means of local hyperaemia determines the growth of the pigmentless hair instead of the normal chocolate-black. So we see that on the ears and feet as well as on the back and sides we obtain the temperature pigment-producing reaction. The different parts of the body of the Siamese cat have however a different "sensibility" to low temperature. While it is easy to obtain pigmentless hair on the back by means of a simple warming by wadding and a cotton bandage, on the ear and

foot this decrease of heat loss is not sufficient and it is necessary to warm the ear not only by diminishing the heat-loss but also by increasing the heat production *i. e.* to apply stronger agents inducing local hyperaemia. According to the data obtained by one of the authors in the Himalayan rabbit and the Himalayan Guinea pig[6,7,8] it is possible to say that the different parts of the body of the Siamese cats are non-homogeneous, viz. have different thresholds of irritation in relation to the pigment production. In this case the threshold of irritation is understood as the minimal external "temperature" or: the minimal "temperature of the surroundings" when the pigment formation in the hair does not take place. The male of the Siamese cat has the threshold of irritation of the back tissue—(in the region of shoulders) about + 37°C and the female about + 36°C. The thresholds of irritation of the other regions of the back are accordingly lower (about + 30°C + 32°C) as it is easier to induce the growth there of pigmentless or slightly pigmented hair. The degree of threshold of irritation of the ear cannot be defined exactly. But considering that local hyperaemia of the ear in the Himalayan rabbit—as was shown earlier[7,8]—decreases the threshold of irritation more than 14°C it is possible to suppose the threshold of irritation for the ear to be not less than + 50°C + 51°C and probably even higher, about + 60°C. The threshold of irritation of the foot lies probably between the threshold of the back and ears. Probably it is not less than + 43-45°C.

So we see that the Siamese cat from the point of view of the mechanics of development is analogous to the Himalayan rabbit. The cat as well as the rabbit has different thresholds of irritation for different parts of the body.

A greater similarity is shown by these two races in the process of normal individual development of pigmentation. The first fur of the Himalayan rabbit is pure white and the same is true of Siamese kittens at birth, which fact was already known to cat-fanciers in the ninteenth century[1]. In genetics this fact was first noted by Bateson[2]. The complete absence of pigment in the first fur of the Siamese kittens is without doubt related to the high temperature during intrauterine development and is one more proof of the dependance of the Siamese pigmentation on temperature. In extrauterine development the Siamese kittens, as well as the Himalayan rabbits—under the continual influence of low external temperature, change their first pigmentless pelage for the pigmented one. Thus the age change in the color of pelage is due to the influence of low temperature.

The succession of the normal coloring of the Siamese kittens is interesting because it allows us to estimate the relative heights of the thresholds of irritation for different body-parts. It is evident—and it has been proved by the first of the authors in the Himalayan rabbit—that the succession of pigmentation of the different points corresponds to their place in the series of points with decreasing thresholds of irritation.

Here is an extract from one of the protocols:

September 26, 1927—Five kittens were born of the Siamese cat "Simka." The kittens are covered with a white pigmentless fur.

October 1—The skin of the top of the nose and the skin of the ears becomes brown. In the skin one may see the growing pigmented hair.

October 4—The skin of the top of the nose and the ears is dark brown. Feet and tail are light brown. The new hair is growing rapidly.

October 20—The change of the first fur for the pigmented one is going on rapidly. The color of the body is greyish-white. The middle of the back is light grey. The top of the nose is black. The ears are covered with black hair among which there are a few white contour-hairs. The fore and hind feet

NEW "POINTS" DUE TO LOWERED TEMPERATURE

Figure 11

The dark pigmented hair on the shoulders and on the sides of croup has appeared as the result of the greater heat loss of these body parts due to the bones which underlie these areas.

VARIATION IN REACTION TO TEMPERATURE

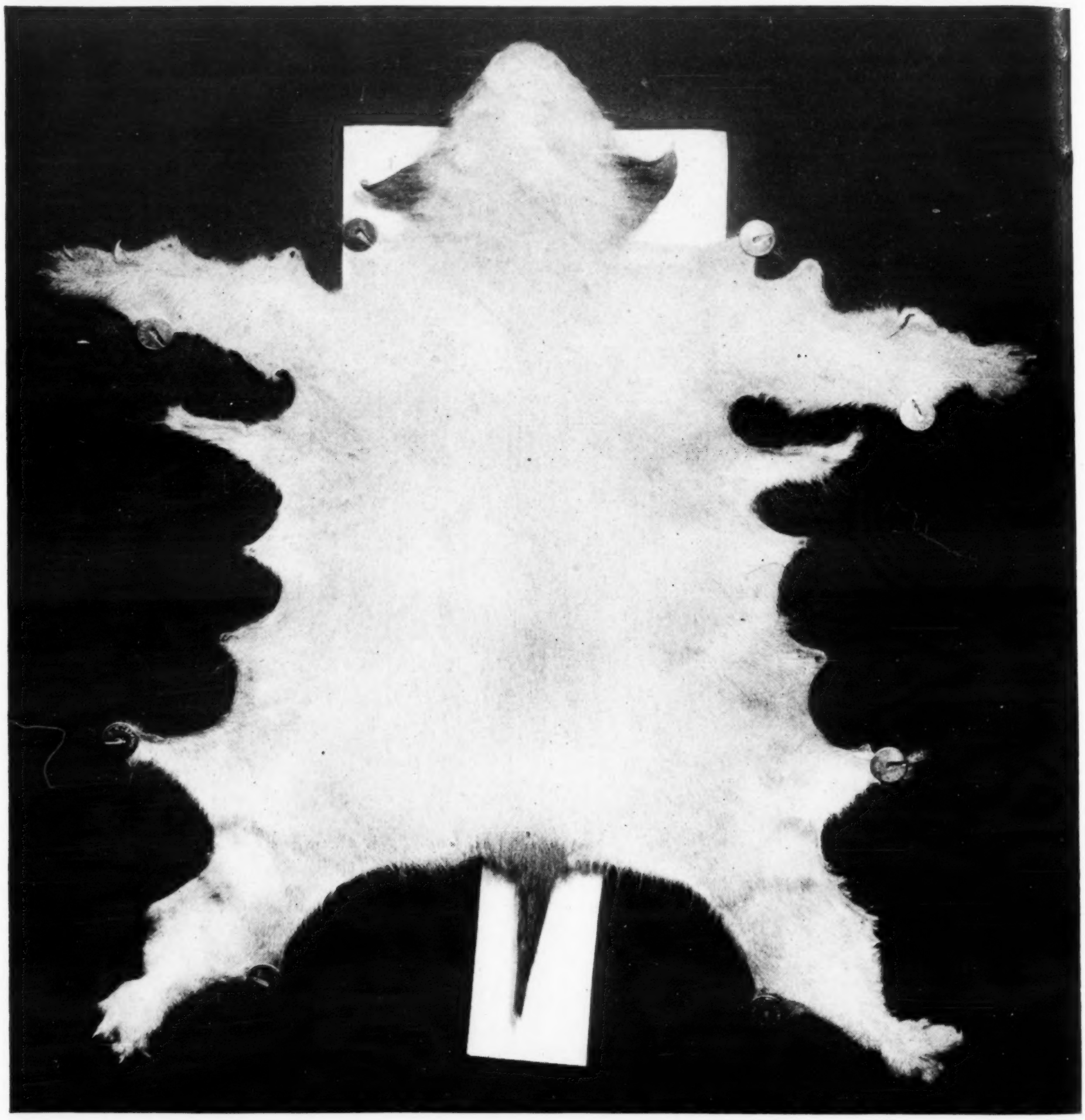
Figure 12

The belly of Siamese cat with almost unpigmented hair; umbilicus is covered with slightly pigmented hair, as a result of the greater threshold of irritation. Different parts of the body vary in their reaction to temperature changes.

are covered with chocolate hair. The tail is covered with chocolate-black hair.

This short description of the succession of coloring permits us to suppose the following series of the parts of the body with decreasing thresholds of irritation: Face (nose) > ears > tail > feet > middle of back > side > belly > armhole.

The conclusion about the relative height of the thresholds of irritation in the body parts indicated by numbers 2, 4, 5, 6, 7, is based on direct experiment, as has already been mentioned. It is interesting to note that the Himalayan rabbit has nearly the same series[7]: nose = tail > ears > hind feet > fore feet > middle of back > side and belly.



WHITE FUR OF SIAMESE KITTEN

Figure 13

The pelage of a Siamese kitten during the change of the first fur to the pigmented one. The ears and the tail have begun to darken, but all the rest of the fur is still white. (Born Sept. 26, 1927, died Oct. 20, 1927.)

Discussion

It is interesting to discuss how far the similarity between the Siamese cat and the Himalayan rabbit extends. Bateson[2] was the first to point out the similarity of these two phenotypes. Wright[14] considers the Siamese pattern as a case of imperfect albinism. Haecker[4] considered it as an example of isabellism. Castle[3] compares their phenotypes and mode of inheritance to that of the Himalayan rabbit, red eyed rat, and non-yellow guinea-pig. We think that the similarities between the Siamese cat and the Himalayan rabbit in inheritable realization and in the temperature reaction, are established clearly by our experiments. In spite of the similarity of these two phenotypes there is a slight difference in the

color, pigment-pattern, and in the eye-color (see Table I). It is necessary to mention that the pigmentless pink eye of the Himalayan rabbit can be made pigmented by experiment, as was shown by W. Shultz[12]. The slightly different pattern, the darker coat-color and the small amount of pigment in the eye of the Siamese cat, are evidently due to the higher thresholds of irritation of the tissues of the Siamese cat in comparison to those of the Himalayan rabbit.

Though the mechanism of development of pigmentation of the Siamese cat is analogous to that of the Himalayan rabbit it is necessary to compare these cats also to other more similar phenotypes. We should like to emphasize the similarity of these cats with the recently studied Marder rabbit[10] placing the phenotype of the Siamese cat between that of the Himalayan and Marder rabbits (see Table I). According to the above the albino series in the cat—in comparison to that of the rabbit may hypothetically be written as follows:

TABLE I—Similarities and Differences of Siamese Cats, Himalayan and "Marder" Rabbits

	Himalayan rabbit	*Siamese cat*	*Marder rabbit*
I—The Color and Pattern			
1. Pattern	acromelanistic +	acromelanistic +	acromelanistic +
2. Body color (back and sides)	white +	cream 0	chocolate —
3. Belly	white +	pale-cream —	pale-cream —
4. Points	chocolate-black +	chocolate-black +	chocolate-black +
5. Yellow pigment	absent +	absent +	absent (?) +
6. Pigment in the iris	absent +	present —	present —
7. Color of the iris	pink +	blue 0	brown —
8. Ruby light of the pupil	.....	present —	present —
II—The Genotypical Peculiarities			
1. Relation to full pigmentation	recessive +	recessive +	recessive +
2. Is it possibly the cryptomere of primitive colors (black, brown, blue)?	yes +	yes +	yes +
III—The Morphogenetics of Pigmentation			
1. The dependance upon temperature	present +	present +	?
2. Hairs at high temperature	white +	white +	?
3. Hairs at low temperature	pigmented +	pigmented +	pigmented +
4. Color of the hairs at low temperature	black / brown (+) / blue	black + / chocolate-black +	black (+) / chocolate-black
5. The dependence upon the heat-regulating mechanism	present +	present +	?
6. Threshold of irritation of the sides	1+2°C & more + (Moscow race)	+30+32°C 0	?
7. Threshold of irritation of the ear	+25+27°C +	>+50° +51°C 0	?
8. Age changes of color	present +	present +	present +
9. First pelage of young	white +	white +	silber-grau (Kosswig)
10. Points in first pelage	non-black (white) +	non-black (white) +	non-black (pale-black)
11. Dependence of the age changes of color upon temperature	present +	present +	?

+Character identical with that of Himalayan rabbit.
—Character identical with that of Marder rabbit.
0 Character specific for Siamese cat.

Rabbit $C > c^{chi} > c^{d} > c^{m} > \text{-------} > c^{h} > c^{a}$
Cat $C > \text{----------} > c^{s} \text{----------}$

(Symbol $c^s = a_1$ of Tjebbes.)

The correctness of this conclusion will be definitely tested when the mechanics of development of pigmentation in the Marder rabbit is studied.

Conclusions

1. The pattern of the Siamese cat is a true acromelanism.

2. The pigmentation of this cat is due to the influence of the external temperature: under the influence of high temperature the hair grows white, under the influence of low temperature it is pigmented.

3. The color and the pattern of the Siamese cat occupies an intermediate position between the phenotypes of the Himalayan and Marder rabbits. In its mode of inheritable realization and temperature reaction it is similar to the Himalayan rabbit and in phenotype is nearer to the Marder rabbit. The inheritable factor producing the Siamese pattern is designated as c^s ($=a_1$ of Tjebbes). The differences between the mechanics of development of pattern of Siamese cats and both rabbit varieties are purely quantitative.

4. The color of the Siamese cat is under a double control: of the external temperature and of the physiological factors determining the heat production and the heat loss.

5. The threshold of irritation in relation to the pigment production is different for different body-parts.

6. The cause of the peculiar pattern of the Siamese cat is non-homogeneity of different tissues, namely the difference in the height of the thresholds of irritation for different body parts.

7. The threshold of irritation of the back tissue of the male evidently is higher than that of the female.

8. The age change of the color in the Siamese kittens is due to the influence of the external temperature.

Author's Note: During the correction of my proofs I came across a very interesting article by Prof. Nachtsheim: "Die Entstehung der Kaninchenrassen in Lichte ihrer Genetik." Nachtsheim also makes a comparison of the phenotypes of the Siamese Cat and the "Marder" Rabbit. From an amiable letter of his I see that quite independently we have both come at the same time to a similar comparison of these two animals: Nachtsheim's (1929) investigation is based on the study of "Marder" Rabbits. ours—(1929) on the study of the Siamese Cat.

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THE PLANT PATENT LAW

ANNOUNCEMENT was made in the February JOURNAL that a law establishing patents for new varieties of plants was under consideration before Congress. Perhaps on account of a desire to "do something for agriculture" the bill encountered little opposition, was passed by Congress in an amended form, and received the President's signature on May 23. The text of the new law (or rather the revision of the old patent law) as finally enacted differs in important respects from that of the bill originally presented, and printed in the February JOURNAL.

The report of the Committee on Patents, to which the bill was referred, was made to Congress on April 13. It presents an excellent statement of the purposes of the bill, and of some of its legal aspects, which will be of considerable interest to readers of the JOURNAL. As the report has not been given very wide circulation it is therefore published in full:

PLANT PATENTS

APRIL 2 (calendar day, APRIL 3), 1930—Ordered to be printed

MR. GOLDSBOROUGH, from the Committee on Patents, submitted the following

REPORT

[To accompany S. 4015]

The Committee on Patents, to whom was referred the bill (S. 4015) to provide for plant patents, have considered the same and report thereon with amendments, and, as so amended, recommend that the bill do pass.

All of the committee amendments except two are clerical in character. As to the two amendments, one adds to the bill the usual separability clause and the other eliminates from the scope of the bill patents for varities of plants which exist in an uncultivated or wild state, but are newly found by plant explorers or others.

I. Purposes of the Bill

The purpose of the bill is to afford agriculture, so far as practicable, the same opportunity to participate in the benefits of the patent system as has been given industry, and thus assist in placing agriculture on a basis of economic equality with industry. The bill will remove the existing discrimination between plant developers and industrial inventors. To these ends the bill provides that any person who invents or discovers a new and distinct variety of plant shall be given by patent an exclusive right to propagate that plant by asexual reproduction; that is, by grafting budding, cutting, layering, division, and the like, but not by seeds.

Stimulation of Plant Breeding

To-day the plant breeder has no adequate financial incentive to enter upon his work. A new variety once it has left the hands of the breeder may be reproduced in unlimited quantity by all. The originator's only hope of financial reimbursement is through high prices for the comparatively few reproductions that he may dispose of during the first two or three years. After that time, depending upon the speed with which the plant may be asexually reproduced, the breeder loses all control of his discovery. Under the bill the originator will have control of his discovery during a period of 17 years, the same term as under industrial patents. If the new variety is successful, the breeder or discoverer can expect an adequate financial reward. To-day plant breeding and research is dependent, in large part, upon Government funds to Government experiment stations, or the limited endeavors of the amateur breeder. It is hoped that the bill will afford a sound basis for investing capital in plant breeding and

consequently stimulate plant development through private funds.

In addition, the breeder to-day must make excessive charges for specimens of the new variety disposed of by him at the start in order to avail himself of his only opportunity for financial reimbursement. Under the bill the breeder may give the public immediate advantage of the new varieties at a low price with the knowledge that the success of the variety will enable him to recompense himself through wide public distribution by him during the life of the patent. The farmers and general public that buy plants will be able promptly to obtain new improved plants at a more moderate cost.

Economic Benefit to Agriculture and the Public

The food and timber supply of the Nation for the future is dependent upon the introduction of new varieties. Many millions of Federal and private funds are annually spent in combating disease through plant quarantines, disinfection, spraying, and other methods. The phoney peach disease has threatened the important peach supply of Georgia and the welfare of one of the most important industries of that State. The chestnut blight has wiped the eastern forests clean of the valuable chestnut tree. The white pine blister rust threatens the white-pine forests. The plant pathologist has through his experiments attempted with but slight success to combat these plant diseases. But an equally valuable means of combating plant disease is the development of new disease resistant varieties by the plant breeder. The bill proposes to give the breeder the incentive to develop such varieties without the aid of Federal funds.

Similarly, the development of drought-resistant and cold-resistant varieties of plants is of great importance to agriculture. An apple with greater resistance to cold is one of the demands of the northern portion of the country. We must look to the plant breeder for an acceptable substitute for rubber. The improvement of medicinal plants is an unexplored field. The spectacular development of new classes of plants, such as the loganberry and many of Burbank's products, is only a small part of the economic benefit to the country afforded by successful plant breeding.

No one will question the fact that new varieties of food, medicinal, and other economic plants may be an important factor in maintaining public health and in promoting public safety and national defense. Thus the food supply of the Nation, both from the viewpoint of the producer and the user, is of vital importance, and insurance against failure in that supply is necessary to public safety and national prosperity. Plant breeding and discovery, while in its infancy, is fundamentally connected with the Nation's food supply, and will, if encouraged and developed, be of incalculable value in maintaining public health and prosperity, and in promoting public safety and the national defense. Finally, plant patents will mean better agricultural products that will give the public more actual value for its dollar.

II. Bill Generally Advocated

The proposed legislation was originally introduced by Senator Townsend as S. 3530 of this session. The present measure is substantially the same as the original bill except for the elimination of patents for certain newly found plants and the granting of patents irrespective of the fact that the plant may, under some conditions, reproduce itself without human aid.

The proposed legislation has been generally advocated. The Secretary of Agriculture, whose letter appears in full in Appendix A to this report, states that—

> The proposed legislation would appear to be desirable and to lend far-reaching encouragement to agriculture and benefit to the general public.

Mr. Thomas A. Edison states that—

> Nothing that Congress could do to help farming would be of greater value and per-

manence than to give to the plant breeder the same status as the mechanical and chemical inventors now have through the patent law. There are but few plant breeders. This [the bill] will, I feel sure, give us many Burbanks.

The proposed legislation has been endorsed by former Secretary of Agriculture Jardine, the National Horticultural Council, the American Association of Nurserymen, the American Farm Bureau Federation, the National Grange, and many State commissioners of agriculture, experiment station officials, and individual growers and nurserymen.

III. Explanation of Provisions of Bill

Classes of New Varieties

New and distinct varieties fall into three classes—sports, mutants, and hybrids.

In the first class of cases, the sports, the new and distinct variety results from bud variation and not seed variation. A plant or portion of a plant may suddenly assume an appearance or character distinct from that which normally characterizes the variety or species.

In the second class of cases, the mutants, the new and distinct variety results from seedling variation by self pollenization of species.

In the third class of cases, the hybrids, the new and distinct variety results from seedlings of cross pollenization of two species, two varieties, or of a species and a variety. In this case the word "hybrid" is used in its broadest sense.

All such plants must be asexually reproduced in order to have their identity preserved. This is necessary since seedlings either of chance or self-pollenization from any of these would not preserve the character of the individual.

These cultivated sports, mutants, and hybrids are all included in the bill, and probably embrace every new variety that is included. The exclusion of a wild variety, the chance find of the plant explorer, is in no sense a limitation on the usefulness of the bill to those who follow agriculture or horiculture as a livelihood and who are permitted under the bill to patent their discoveries.

Patent Grants Right of Asexual Reproduction Only

Whether the new variety is a sport, mutant, or hybrid, the patent right granted is a right to propagate the new variety by asexual reproduction. It does not include the right to propagate by seeds. This limitation in the right granted recognizes a practical situation and greatly narrows the scope of the bill. Whether the new variety is a hybrid, mutant or sport, there is never more than one specimen of it produced except through asexual reproduction. For example, without asexual reproduction there would have been but one true McIntosh or Greening apple tree. These varieties of apple could not have been preserved had it not been through human effort in the asexual reproduction of the two original trees. They could not have been reproduced true to the type by nature through seedlings. The bill, therefore, proposes to afford through patent protection an incentive to asexually reproduce new varieties. Many varieties of apples equally as valuable as the McIntosh or Greening have undoubtedly been created and disappeared beyond human power of recovery because no attempt was made to asexually reproduce the new varieties. The present bill by its patent protection proposes to give the necessary incentive to preserve new varieties. On the other hand, it does not give any patent protection to the right of propagation of the new variety by seed, irrespective of the degree to which the seedlings come true to type.

Distinct Varieties

The bill authorizes the grant of a patent only in case the new variety is distinct. It is not necessary that the new variety be a new species, but the bill does not exclude a new and distinct species from being patented. On the

other hand, in order for the new variety to be distinct it must have characteristics clearly distinguishable from those of existing varieties, and it is immaterial whether in the judgment of the Patent Office the new characteristics are inferior or superior to those of existing varieties. Experience has shown the absurdity of many views held as to the value of new varieties at the time of their creation.

The characteristics that may distinguish a new variety would include, among others, those of habit; immunity from disease; resistance to cold, drought, heat, wind, or soil conditions; color of flower, leaf, fruit, or stems; flavor; productivity, including everbearing qualities in case of fruits; storage qualities; perfume; form; and ease of asexual reproduction. Within any one of the above or other classes of characteristics the differences which would suffice to make the variety a distinct variety, will necessarily be differences of degree. While the degree of difference sufficient for patentability will undoubtedly be a difficult administrative question in some instances, the situation does not present greater difficulties than many that arise in the case of industrial patents.

In specifying the differences in characteristics the Patent Office will undoubtedly follow the practice among botanists in making use of verbal descriptions and photographic and other reproductions, taking some known plant as a basis of comparison. Modern methods of identification, together with such amplification thereof as may reasonably be expected, will render it possible and practicable to describe clearly and precisely the characteristics of a particular variety. When this can not be done by an applicant for a patent, the variety is not clearly distinguishable as a distinct variety, and no patent would issue.

Of course, allowance must be made for those minor differences in characteristics commonly called fluctuations, which follow from variations in methods of cultivation or environment and are temporary rather than permanent characteristics of the plant.

Exception of Tuber-Propagated Plants

The bill excepts from the right to a patent the invention or discovery of a distinct and new variety of a tuber-propagated plant. The term "tuber" is used in its narrow horticultural sense as meaning a short, thickened portion of an underground branch. It does not cover, for instance, bulbs, corms, stolons, and rhizomes. Substantially, the only plants covered by the term "tuber-propagated" would be the Irish potato and the Jerusalem artichoke. This exception is made because this group alone, among asexually reproduced plants is propagated by the same part of the plant that is sold as food.

The Prerequisite of Asexual Reproduction

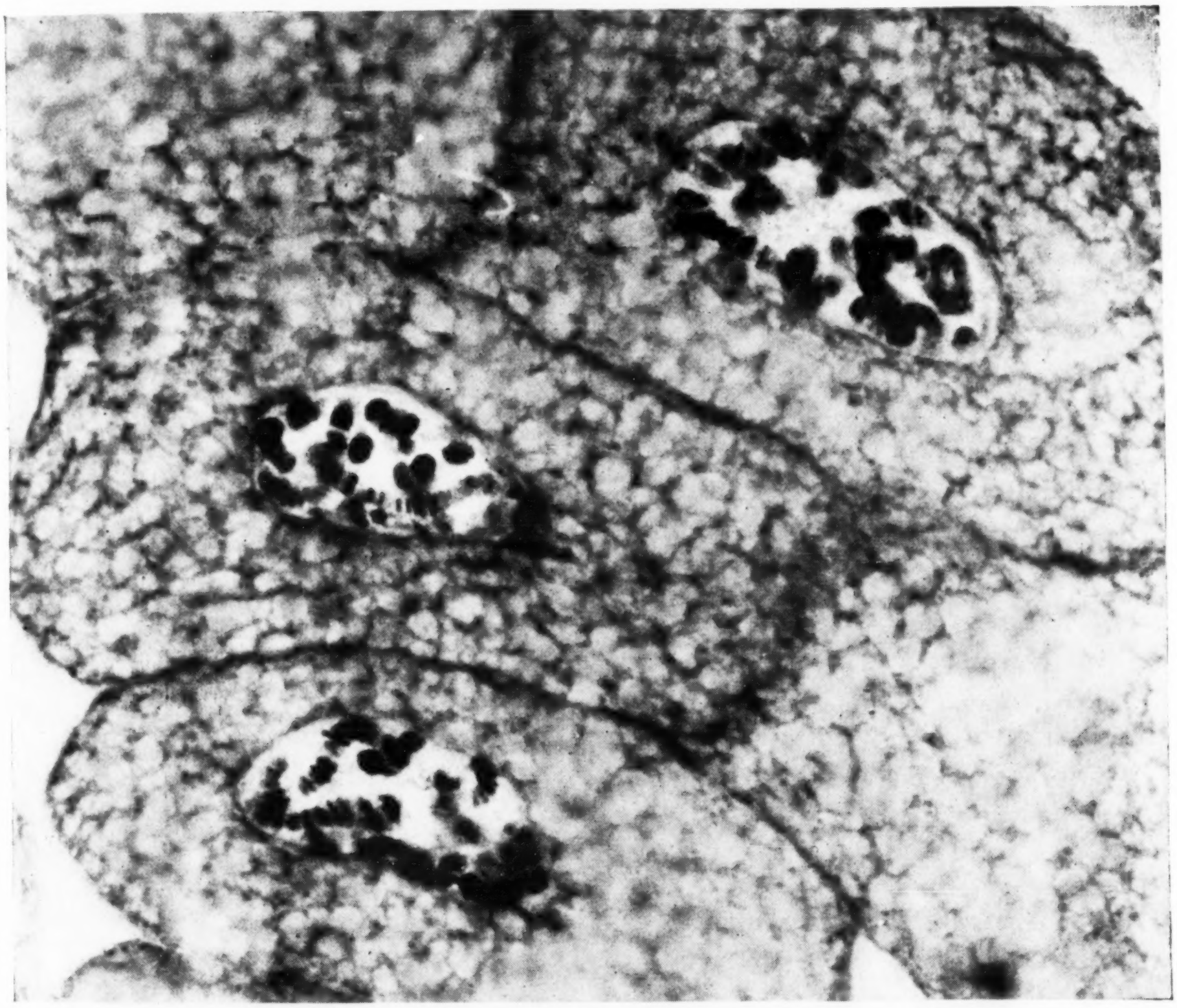
It is not only necessary that the new and distinct variety of plant shall have been invented or discovered, but, it is also necessary that it shall have been asexually reproduced prior to the application for patent. A plant patent covers only the exclusive right of asexual reproduction, and obviously it would be futile to grant a patent for a new and distinct variety unless the variety had been demonstrated to be susceptible of asexual reproduction. Of course, theoretically under laboratory conditions it is probable that all plants can be asexually reproduced, but it is hardly to be expected that a patent will be applied for unless at the time of application the plant can be asexually reproduced upon a commercial scale or else there is a reasonable expectation that it can be so reproduced in the near future.

(The remainder of the report, dealing chiefly with the legal phases of the bill, and the text of the law as enacted, will appear in the next number of the JOURNAL.)

DISCOID STRUCTURE OF THE SPIREME

And Irregular Cell Division in *Drosophila Melanogaster*

DONTCHO KOSTOFF
Sofia University, Bulgaria



HETEROGENEOUS CHROMOSOME STRUCTURE

Figure 14

The linear arrangement of the genes necessitates the assumption that the chromosomes are made up of chemically different components. The discoid structure of the chromosomes shown in this photograph, indicates the existence of such chemical differences in the varying capacity to absorb haematoxylin. These discs may represent the actual packets in which inherited characters are passed from generation to generation.

DURING the last fifteen years the Morgan school of genetics[5] working with *Drosophila* have advanced the idea of linear arrangement of the hereditary units in the chromosomes, and by calculating the frequency of crossings over have even drawn chromosome maps. Recently, many investigators working with various organisms have come to the same conclusion. The assumption of the linear arrangement of the genes

requires heterogeneous structure of the chromosomes. Such a structure was found in the spireme of *Drosophila melanogaster* (Figure 14). The spiremes illustrated in the figure have a discoid structure, the disks differing in respect to their capacity to absorb haematoxylin so that there is a gradation series between the black disks and those that absorbed no stain. From the differential staining behavior of these chromatin disks one can conclude that they are, or contain, chemical compounds (apparently proteins) of diverse nature.

Discoid type of spireme structure was also observed by Balbiani[1] in *Chironomus*. The discoid structure of the chromosomes of *Drosophila* was not observed during the metaphase and anaphase. During these phases they appear smooth and homogeneous like those reported by Bridges[2] and others. Presumably there is an exchange of substances occurring among the disks during the late prophase, so that the heterogeneity of the chromosomes and their differential behavior to stains is masked in the following phases.

In the pupal stage, occasionally, chromosomes were found lagging on the spindle during the anaphase in the somatic and generative cells. Jeffrey and Hicks[3] found irregular meiotic figures and explained these irregularities by postulating hybrid nature of *Drosophila melanogaster*. Kostoff and Kendall[4] reported frequent irregular mitotic divisions in Cynipid pupae. Such irregularities might have, however, some other plausible interpretation. Perhaps the agents responsible for the irregular cell division in pupae are the autolytic ones that are so abundant during this stage, since it is well known that agents of various nature can disturb the processes of cell division.

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2. Bridges. C. B. 1927. Constrictions in the chromosomes in *Drosophila melanogaster*. *Biolog. Zentrbl.*, 47:600-603.

3. Jeffrey, E. C. and G. C. Hicks. 1925. The reduction division in relation to mutation in plants and animals. *Amer. Natur.*, 59:410-426.

4. Kostoff, Dontcho and James Kendall. 1929. Studies on the structure and development of certain Cynipid galls. *Biol. Bull.*, 56:402-459.

5. Morgan, T. H. 1926. The theory of the gene. Yale Univ. Press. 1926.

Books Received

BOOKS are acknowledged in this column as received, and such acknowledgment must be regarded as sufficient return for the courtesy of the sender. As far as space permits, books that contain material of special interest to the readers of the Journal *will be reviewed in later numbers.*

A HISTORY OF SCIENCE, and its Relations with Philosophy and Religion, *by* William Cecil Dampier Dampier-Whetham, Fellow and Sometime Senior Tutor of Trinity College, Cambridge. New Edition, Revised and Corrected. Pp. 514. 10 Chapters. Price, $4.00. The Macmillan Co., New York. 1930.

RIDERS OF THE PLAGUES, The Story of the Conquest of Disease, *by* James A. Tobey, Doctor of Public Health. Pp. 348. 12 Chapters. 8 Illustrations. Price, $3.50. Charles Scribner's Sons, New York. 1930.

HUMAN BIOLOGY AND RACIAL WELFARE. *By* 27 Contributors. *Edited by* Edmund V. Cowdry, Ph.D., Professor of Cytology, Washington University, St. Louis. Pp. 612. 25 Chapters. 5 Parts. Price, $6.00. Paul B. Hoeber, Inc., New York. 1930.

GENETICS OF COTTON

A Survey of Our Present Knowledge

THOMAS H. KEARNEY

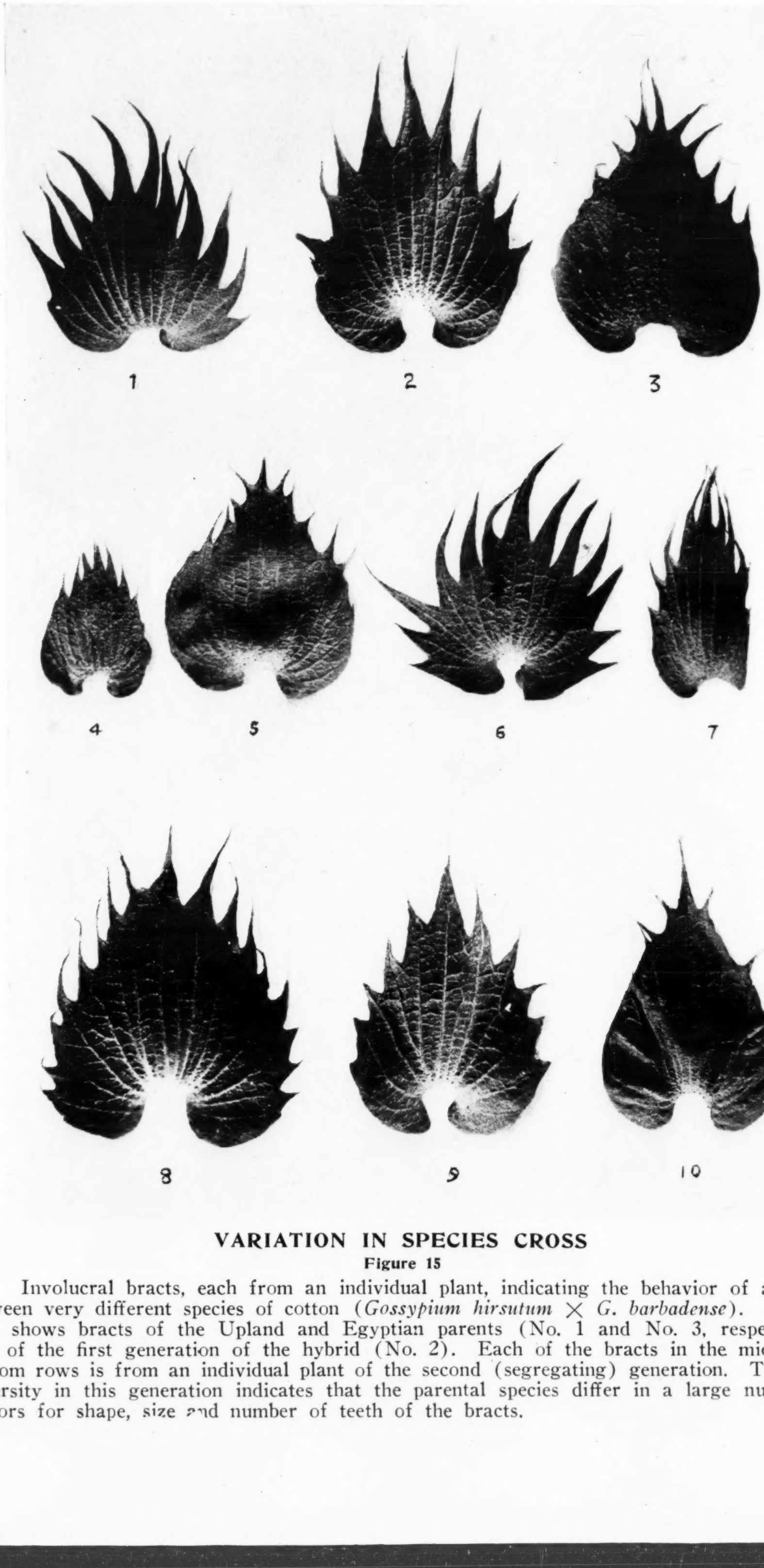
THE genus Gossypium, comprising the wild and cultivated cotton plants of the world, is an attractive subject for genetic investigation. Several very distinct species are in cultivation and the species within each of the main groups of cultivated cottons, American and Asiatic, can be intercrossed without difficulty. As was pointed out in an earlier paper, there also exist, in tropical and subtropical countries, truly wild species of Gossypium whose relationship to the cultivated cottons is obscure (Kearney,[30] *). Genetic research doubtless would clear up some of the taxonomic problems in this group.

The large size of the cotton flower and the readiness with which controlled self-fertilization and cross-fertilization can be effected are important advantages from the point of view of geneticists and plant breeders. It is also an advantage that all parts of the plant are so large as to make it easy to measure the characters. On the other hand, the long duration of the growing and flowering periods are disadvantages in connection with inheritance studies, since most of the characters are very sensitive to the influence of changes in weather conditions and consequently fluctuating variation often obscures the results of the action of genes.

Examination of the fairly extensive literature on inheritance of characters in cotton shows that surprisingly few of them have been found to be inherited in a definitely alternative manner. This is partly due to the facts that genetic studies have been carried on chiefly in connection with practical breeding work and that most of the characters in which the cotton breeder is interested, such as size of the bolls and length and abundance of the lint, are conditioned by several factors. Like most "quantitative" characters, their frequency distributions in F_2 show only a single mode.

Another reason why few examples of simple Mendelian inheritance have been recorded has been pointed out recently by S. C. Harland, who notes that students of the genetics of cotton have worked largely with crosses between different species. (Figures 15 and 16) Harland found that characters such as color of the pollen and presence or absence of the petal spot, which show monohybrid segregation in crosses within a species, exhibit the "quantitative" type of inheritance in crosses between different species. He concludes that "species hybrids in cottons differ from varietal hybrids in the extent to which differences occur in modifying factors. In a species hybrid each main gene is apparently accompanied by a group of modifiers which have the effect of diluting the character in steps down to the recessive"[20] (p. 399). In another paper this conclusion is re-stated as follows: "In varietal crosses there is segregation of the main gene alone, whereas in the inter-specific cross there is segregation of modifiers which may partially, or in some cases entirely, obscure the distinction between dominant and recessive. There is thus no real difference in the mechanism of inheritance in inter-specific, from that which exists in varietal crosses."[23] (p. 17). Harland also found that when F_1 of an inter-species hybrid was backcrossed on the parent possessing the full complement of plus modifiers,

*Numbered references refer to "Literature Cited," which will appear at the end of the article in the following number of the JOURNAL.



VARIATION IN SPECIES CROSS

Figure 15

Involucral bracts, each from an individual plant, indicating the behavior of a hybrid between very different species of cotton (*Gossypium hirsutum* × *G. barbadense*). The top row shows bracts of the Upland and Egyptian parents (No. 1 and No. 3, respectively), and of the first generation of the hybrid (No. 2). Each of the bracts in the middle and bottom rows is from an individual plant of the second (segregating) generation. The great diversity in this generation indicates that the parental species differ in a large number of factors for shape, size and number of teeth of the bracts.

clear-cut monohybrid segregation in F_2 often resulted.

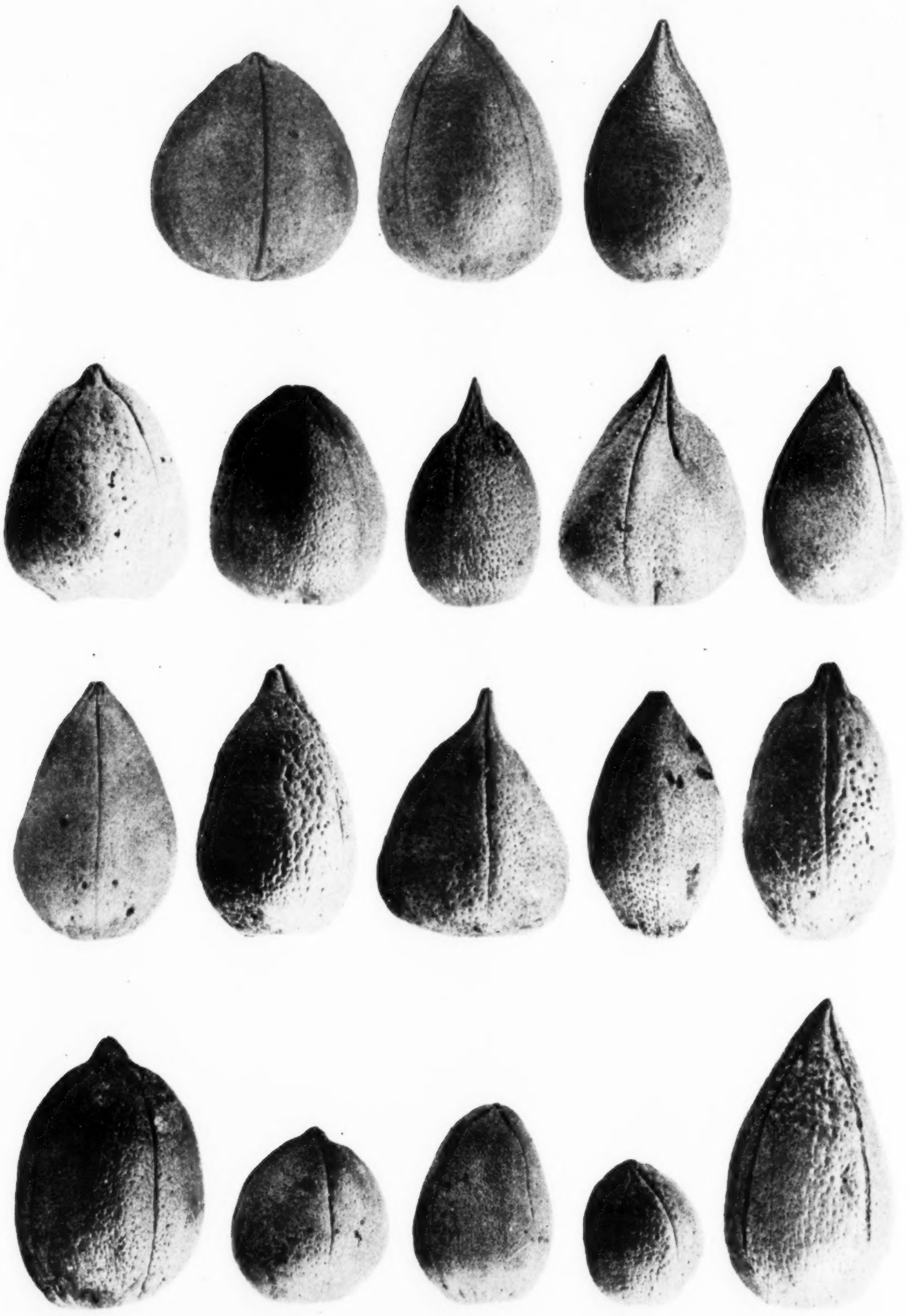
The haploid number of chromosomes is 13 in the Asiatic group and 26 in all cultivated cottons of the American group, so far as is known. Harland[18] states that "inheritance in New World cottons appears to be far more complex than in the Asiatic group" and that "the more complicated type of inheritance in New World cottons is in some way a consequence of the higher chromosome number." It should be noted, however, that he is comparing here the behavior of crosses between very distinct species of the American group, such as Upland and Sea Island, with the behavior of crosses between Asiatic cottons that are much more nearly related to one another, and presumably differ less in their complements of modifying factors. Harland has elsewhere expressed the opinion that "there is only one species of cultivated Asiatic cotton."[15]

Mutation in a single gene, by which, presumably, have arisen the characters showing simple Mendelian inheritance in crosses with the normal form, appears to be much less frequent in cotton than in such organisms as maize among plants and Drosophila among animals. Only three examples, and these all in Sea Island cotton, are given by Harland, "the types white flower, naked seed and crinkled dwarf"[20] (p. 398) but naked-seed forms are of rather frequent occurrence in Upland cotton, also. To this list probably should be added the narrow-lobed or okra leaf and the red leaf variant in Upland cotton, and two variants in Egyptian cotton, one characterized by absence or very weak development of the petal spot, the other by very restricted development of the fuzz on the seed. The latter has been found also in Upland cotton and was designated "fuzzy tip" by Carver[8]. Other variants, usually of a more or less degenerate nature, are observed in all types of cotton and some of these may have originated by mutation. Decidedly off-type plants have appeared occasionally in inbred families of Egyptian cotton in Arizona (Figures 17-18) but owing to the complete sterility of the plants the inheritance of the characters could not be investigated. A less degenerate variant, "short branch", in Pima Egyptian cotton, characterized by reduction of the fruiting branches to a single developed internode, when crossed with the normal form, showed clear-cut Mendelian segregation (Kearney[29]).*

This paper presents a summary of the data on the few characters of the cotton plant for which more or less convincing evidence of monohybrid or dihybrid inheritance has been adduced. The very scanty available information on linkage relations in Gossypium is also considered. No attempt is made to review the rather copious literature of characters showing the "quantitative" type of inheritance and presumably conditioned by several factors, since the data throw no additional light on the relations of the genes. The inheritance of such characters was treated at some length in an earlier publication (Kearney[27], figures 3-41, pp. 33-39).

The following list comprises all proven or strongly indicated examples of allelomorphic characters in cotton known to the writer. These are con-

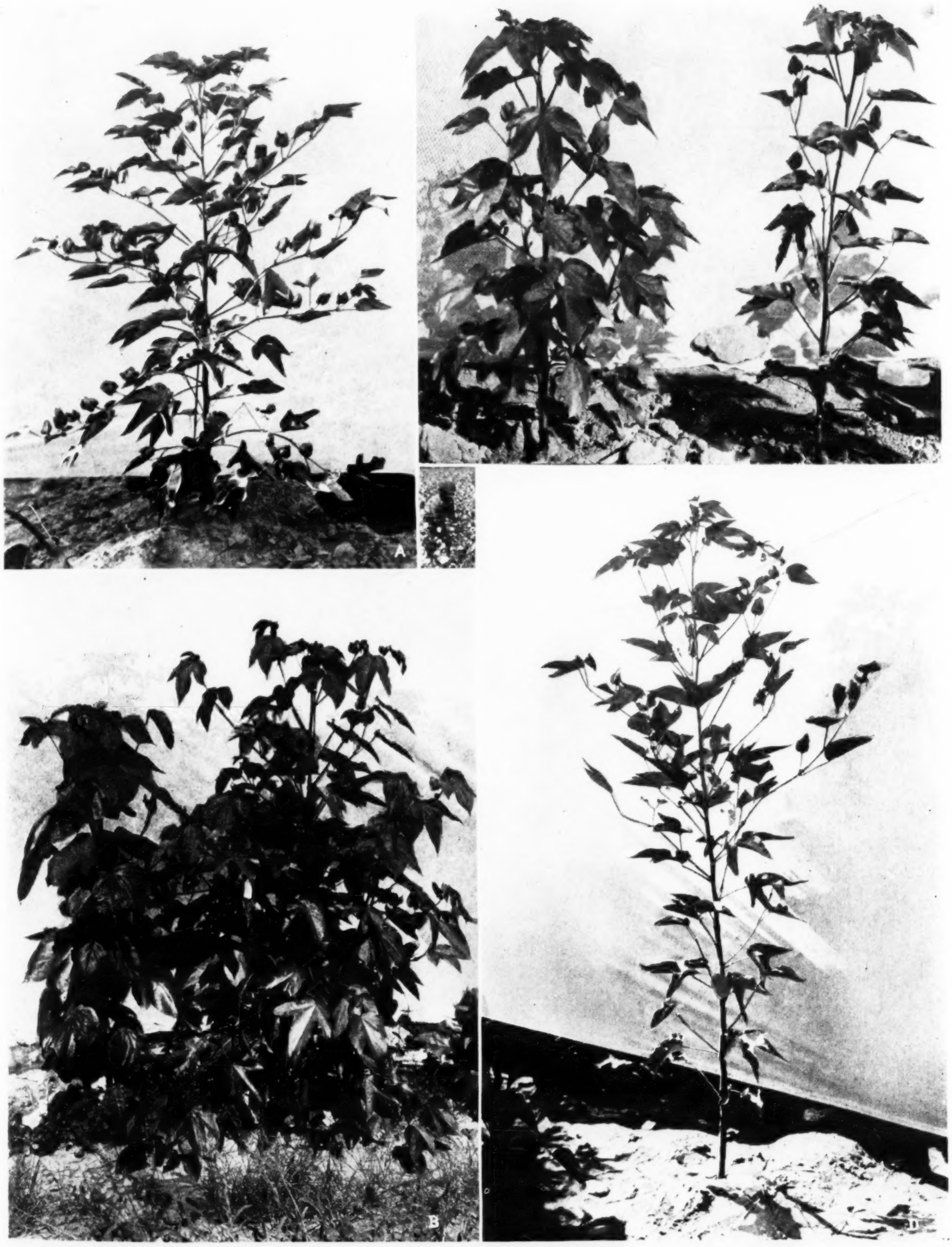
* One of the best authenticated examples of origin by mutation of a variation in cotton is described as follows by Harland[21]: "Sea Island White has been known for a long time to occur as a mutant in reputedly pure lines of Sea Island cotton which have undergone self-fertilization for 12 generations in St. Vincent, and are homozygous for yellow. Occasionally a single white-flowered plant occurs in a progeny row, and is always found to breed true. That it is a true mutant of the ordinary 'loss' type, probably at a single locus in a chromosome, is shown by the fact that on their first appearance such white-flowered forms never occur in Mendelian proportions, and that a cross with parental yellow exhibits the ordinary type of monohybrid behavior, white being a simple recessive." (p. 101).



BOLL CHARACTERS IN SPECIES CROSS

Figure 16

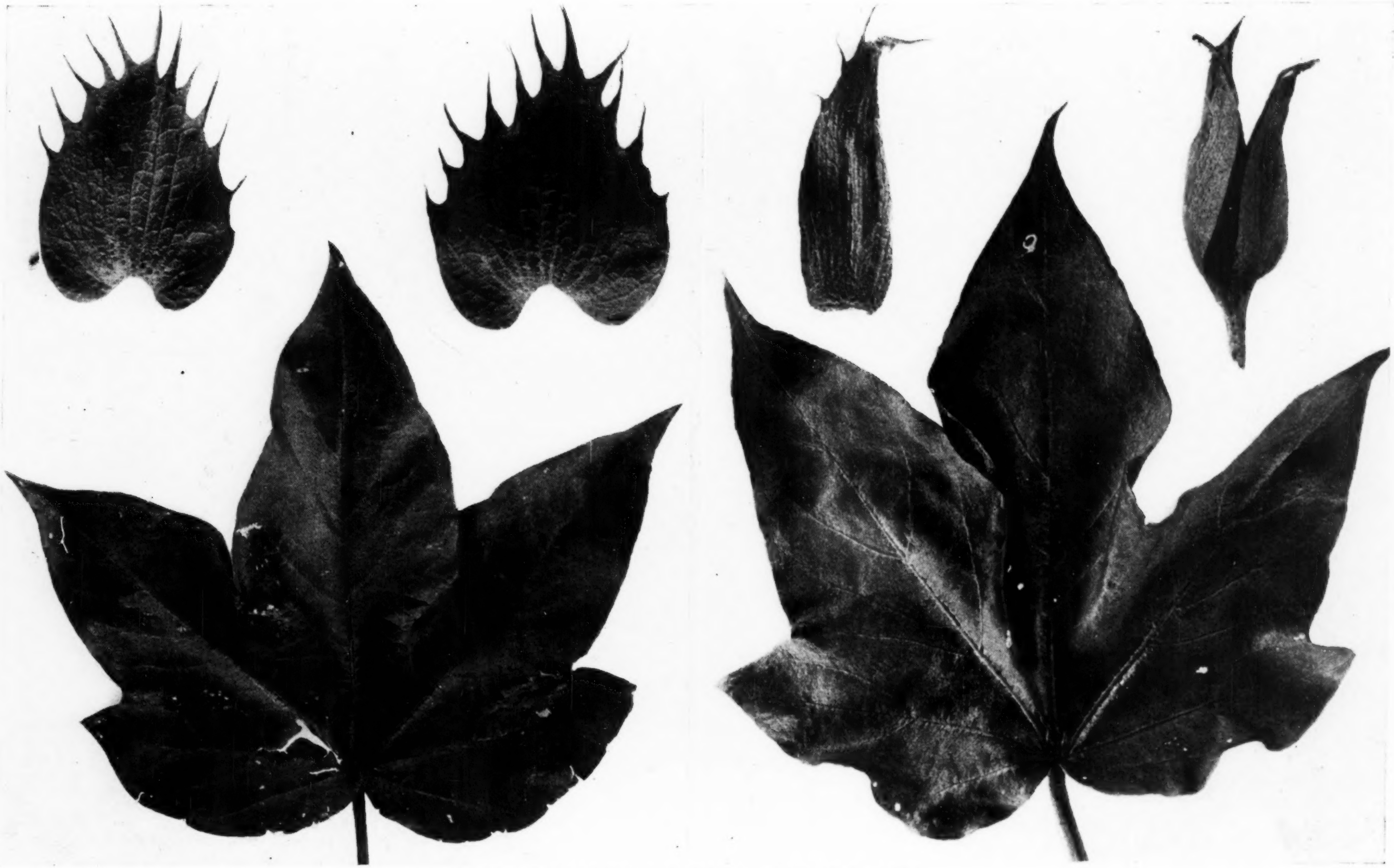
Bolls of the same interspecies hybrid illustrated in figure 15, the top row representing the parent species (Upland left, Egyptian right) and first generation of the hybrid (center). Each of the bolls in the other three rows is from an individual plant of the second generation. Difference between the parent species in respect to many factors for shape, size and surface of the boll is indicated.



NORMAL AND "ROGUE" COTTON PLANTS

Figure 17

A—A normal, very fertile plant of Pima cotton, to be compared with rogue plants shown at *B*, *C*, and *D*. *B*—A "rogue" plant (left) which appeared in the first generation of a cross between two inbred Pima families neither of which had produced any plants of abnormal appearance. The plant at the right was typical of the rest of the F_1 progeny. The rogue was completely sterile and its leaves were abnormally broad and thick. *C*—A rogue plant (right) which appeared in the eighth inbred generation of a family of Pima Egyptian cotton. The population comprised 239 individuals, of which only the one plant was off-type, all the others resembling the plant to the left. The rogue was characterized by complete sterility, slenderness, erect branches, small narrow leaves and narrow involucral bracts with very few teeth. *D*—The rogue plant shown in *C* (right) photographed one month later.



VARIATION IN LEAVES AND BRACTS

Figure 18

Leaf and involucral bracts of a rogue very similar to the one shown in Figure 17*C*, which appeared in an otherwise normal family of Pima cotton. The abnormal narrowness of the leaves and involucral bracts, the latter with teeth greatly reduced in number and size, are evident by comparison with the normal type at left. The rogues shown here and in Figure 17 probably originated by mutation, but their complete sterility precluded further investigation.

sidered on the following pages in the order in which they are listed, together with a few characters in regard to which the evidence is inconclusive.*

Plant "crinkle leaf dwarf," plant normal
Short branch, normal branch.
Chlorophyll locally deficient, chlorophyll evenly distributed.
Leaf color red, leaf green.
Leaf lobes narrow (okra leaf), leaf lobes wide.
Petal color whitish, petals yellow.
Petal color whitish or yellow, petals red.
Petal spot absent or weak, petal spot strongly developed.
Pollen color whitish, pollen yellow.
Boll apical furrow present, furrow absent.
Seeds fuzzy, seeds naked.
Seeds entirely fuzzy, seeds fuzzy at tip.
Seed fuzz white, seed fuzz green.
Seed fuzz white, seed fuzz brown.

Plant Type

A type of plant designated "Crinkle Leaf Dwarf" is described as follows by Harland[12]:

> In September, 1915, the writer noticed in a plot of selected Sea Island cotton certain rogue plants, all of which possessed the same general morphological characters . . . The main stem ceases to grow at a very early stage, so that the maximum height is less than 2 feet 6 inches. The plants are often without monopodial branches [limbs] but one or two of the latter, about equal in size to the main stem, may be present . . . . The tendency to boll shedding in the rogues is so pronounced, however, that 95 per cent of the bolls were shed. In other plants all the bolls dropped. The leaves are much smaller than those of Sea Island. They possess a peculiar appearance owing to patches of lighter yellowish-green being distributed over the surface. The leaves invariably have torn and ragged edges, and are characteristically crinkled. There is a general reduction in the size of all the vegetative parts. The internodes, the teeth of the bracts (Plate 1), the length of the lint, and the flower parts are all shortened.

Progenies grown from selfed seed contained only rogues and the type bred true for 4 generations. Crosses of the rogue with the normal form gave an F_1 that was uniform and indistinguishable from normal Sea Island. In F_2 there were 173 Sea Island and 53 rogue plants. It was concluded that the rogue characters are due to retrogressive mutation of a single gene, the slight deficiency of rogue plants being attributed to their weaker constitution. Progeny tests of 68 normally-appearing F_2's proved 22 to be homozygous and 46 heterozygous.

Branch Length

Kearney[29] found that the descendants of a presumable mutant in Pima Egyptian cotton, "Short Branch," characterized by fruiting branches of only one developed internode, when crossed with normal Pima plants having fruiting branches of several internodes, showed typical monohybrid behavior, without dominance. (Figure 19). The F_1 plants had branches of 1, 2 or 3 internodes. An F_2 progeny of one of them was grown and gave a fair approximation to a 1:2:1 ratio. F_3 progenies were grown from F_2 individuals as follows: 2 which had only 1-internode branches, 2 which had not fewer than 4 internodes on the longest branch and 4 which had 2 or 3 internodes on the longest branch. It was assumed that the first class was homozygous for "short branch," the second class homozygous for long or normal branch and the third class heterozygous. The behavior in F_3 confirmed these assumptions, there being no segregation in the progenies of "short branch" and "normal branch" F_2s and the 4 progenies of intermediate F_2s having segregated into the three classes, with a fair approximation, in the combined population, to a 1:2:1 ratio.

Chlorophyll Deficiency

The only published data on inheritance of this character in cotton appear to be those of Stroman and Mahoney[44] and Harland[22]. The former interpret their results as indicat-

*In the list, the recessive allelomorph of each pair is given first, if dominance occurs. Where dominance does not occur, the aberrant, presumably mutant, phase of the character is given first.

gure 17 probably originated
rogues shown here and in Figure
evident by comparison with the normal type at left. The re
and size, are evidently
by mutation, but their complete sterility precluded further investigation.

NORMAL AND "SHORT-BRANCH" COTTON PLANTS

Figure 19

At the left is shown a plant of a family of Pima cotton having well-developed fruiting branches, which furnished the normal parent of the cross with the "Short Branch" form. This plant was photographed on the same date as the "short branch" plants shown at the right. The "short branch" family of Pima cotton is characterized by reduction of the fruiting branches to a single developed internode. The "short branch" character showed monohybrid inheritance in crosses with the normal form. It originated, presumably, as a single gene mutation.

ing that an extreme type of chlorophyll deficiency which appeared in a hybrid between Upland and Egyptian cottons is conditioned by two recessive factors. The departures from a dihybrid ratio are rather pronounced, however, and the lethal nature of the character makes it difficult to study, the plants presumably homozygous for chlorophyll deficiency always dying in the seedling stage.

Harland has not published his evidence but has announced the following conclusion: "There are three factors controlling the ordinary green colour of the leaf, which may be called C^{ha}, C^{hb} and C^{hc}. Any of these factors are sufficient to produce normal green. The first factor is that contained in the Peruvian group, while the other two are found in the Upland group."[22] (P. 313.)

Leaf Color

A dark red color instead of the normal green color of the leaf blade is met with occasionally in Upland cottons (e. g. the variety Wine Sap) as well as in Asiatic cottons and in some of the South American tree cottons. The color usually extends to other parts of the plant, even to the bolls. Crosses between green-leaf and red-leaf Upland cottons have been studied by McLendon[38], Ware[47,48] and Carver[8] and the results have been consistent. In F_1 an intermediate condition exists, the color being less intense and more localized than in the red-leaf parent, while F_2 shows clear-cut 1:2:1 segregation. Similar results were obtained by Leake[36] in crosses within the Asiatic group and by Ware[47] in the interspecies hybrid Egyptian × Upland.

With crosses between Indian cottons having (a) red leaves and red petals and (b) green leaves and yellow petals, Leake[36] obtained results indicating that the red color of both parts may be conditioned by the same gene.

Leaf Pulvinus Color

The pulvinus or "callus" at the base of the leaf blade is usually bright or deep red in Upland cottons (*G. hirsutum*) pink in Sea Island cotton (*G. barbadense*) and greenish or pale brownish green in Egyptian cottons (*G. barbadense?*).

Balls[4] who studied this character in Upland × Egyptian and Kulkarni and Khadilker[34] who studied it in Upland × Sea Island crosses reported an intermediate condition in F_1 and 1:2:1 segregation in F_2. Their data are scarcely conclusive as to clear-cut segregation and Kearney[27] found no evidence of multimodal segregation in F_2 of an Upland-Egyptian hybrid. As with most color characters in interspecies hybrids, in which, presumably, different modifying factors are involved, classification is very likely to be unconsciously biased. The crossing of forms of the same species showing pronounced difference in pulvinus color, if such can be found, would alone give satisfactory evidence as to the mode of inheritance of this character.

Leaf Shape

Crosses between plants having the deeply and narrowly lobed leaf form known as "okra-leaf" in Upland cotton and the broadly and shallowly lobed form which is normal in the same type have been studied by Shoemaker[43] McLendon[38] Peebles and Kearney[41] Carver[8] and Ware[48]. In all cases the inheritance proved to be monohybrid, showing an intermediate shape in F_1 and approximations to a 1:2:1 ratio in F_2. Peebles and Kearney, who crossed ordinary Acala Upland with an Okra-leaf variant of the same variety (Figure 20), found no overlapping of the three classes in F_2, whether the classification was made simply by inspection or by determination of the lobe index (distance from base of leaf to sinus as a percentage of leaf length.) Unpublished data obtained by Peebles on the F_3 of this cross showed fulfillment of the expectation, okra-leaf and normal leaf F_2 individuals breeding true and intermediate individuals segregating approximately 1:2:1.

Similar results were obtained by Leake [35, 36] and by Afzal[1] in crosses between corresponding forms of Asiatic cottons. The data of Afzal, however, who made his cross between forms supposed to represent different species (identified as *G. cernuum* and *G. indicum*) show that the F_2 segregation was less clear-cut, indicating that modifying factors were involved. Kottur[33] in crosses between two Asiatic species, claims monohybrid segregation in respect to the length and the width of the terminal lobe, considered as separate characters.

In interspecific hybrids (Upland × Egyptian) Balls[5] and Kearney[27] found the more deeply lobed (Egyptian) condition dominant in F_1 and absence of clear cut segregation in F_2. In crosses between broad-lobed Upland cottons and the more narrowly-lobed Sea Island cotton, although this is also an inter-specific cross, McLendon[38] found the inheritance to be definitely monohybrid with F_1 intermediate and F_2 segregating 1:2:1. This seems to be the only character in respect to which markedly different behavior has been shown by Upland × Egyptian as compared with Upland × Sea Island.

A case of bud mutation in an Asiatic cotton is reported by Hutchinson ("J. B. H.,")[25]. A plant of deeply and narrowly lobed form of *G. arboreum* designated "Burma Laciniated" produced a branch on which the leaves were broad-lobed. Quoting from the original account: "This mutation has crossed at one step the boundary between *G. arboreum* and G. *Nanking* (see Watt) which Leake [36] has shown is due to a difference in a single

—Photographs by H. F. Loomis.

NORMAL LEAF AND "OKRA-LEAF" FORMS OF ACALA COTTON

Figure 20

Above, a leaf of an okra-leaf variant of the Acala variety of Upland cotton, deeply and narrowly lobed. Below, a leaf of the ordinary form of Acala cotton, shallowly and broadly lobed. When these forms were crossed F_1 was intermediate and F_2 segregated in the ratio 1 narrow: 2 intermediate: 1 broad. Narrow-lobed and broad-lobed F_2s bred true, and the progenies of intermediate F_2s segregated in a 1 : 2 : 1 ratio. Three-fourths natural size.

gene. Since the arboreum (laciniated) type of leaf is dominant to the Nanking type in Trinidad, and since Burma Laciniated has been shown to breed true, it follows that the same mutation occurred in both homologous chromosomes." In this case, as in the Upland-Egyptian crosses, narrow lobe seems to be dominant to broad lobe.

Harland[22], (p. 312) without giving his experimental evidence, makes the following statements concerning the inheritance of leaf shape:

> The laciniated leaf of the Bourbon type, known as Cassava, shows monohybrid inheritance in Upland-Bourbon crosses. Evidence so far points to the existence of a multiple allelomorphic series of factors for leaf-shape with the following terms:
>
> O^u Upland leaf-shape
> O^c Cassava leaf-shape
> O^o Upland Okra leaf-shape
> O^s Upland Super-Okra leafshape
>
> Super-Okra is a type with leaves showing greater laciniation than the ordinary Okra types.

Petal Color

It is to be doubted that pure white petals occur in the genus Gossypium, the color, usually designated "white," which characterizes the Upland cottons and some members of the Asiatic group being really a very pale greenish-yellow. On the other hand, members of the South American tree cotton group, as exemplified by Sea Islands and Egyptians, have normally bright yellow petals.

Fyson[9] in crosses between white-flowered and yellow-flowered Asiatic cottons, reports that yellow was dominant and that 3:1 segregation occurred in some but not all of his F_2 progenies. Leake[36] and Leake and Prasad[37] who also worked with crosses between cottons of the Asiatic group, report that white behaved as a simple recessive to both bright yellow and pale yellow. On the other hand, Kottur[33] crossing a bright yellow-flowered species (*G. herbaceum*) with a white-flowered form, (*G. neglectum* var. *roseum*) both parents being of the Asiatic group, obtained results which Harland[21], (pp. 96-98) interprets as indicating a modified trihybrid ratio.

Burd[7] crossed a white-flowered, presumably mutant form of Sea Island cotton with normal yellow-flowered Sea Island and obtained results which he thought indicated monohybrid segregation obscured by the effects of modifiers for yellow. A similar Sea Island $\times$ Sea Island cross was also studied by Harland[21], (pp. 106, 107) who found the segregation in F_2 to be discontinuous although the ratio was approximately 1:1 rather than 3:1. The population, however, was small (n= 31).

Interspecies hybrids within the American series, between Upland cottons, representing "white," and Egyptian or Sea Island cottons, representing yellow, were studied by Balls[4,5] McLendon[38] Harland[13,21] Kearney[27] and Kulkarni and Khadilker[34] all of whom obtained evidence that in such wide crosses the inheritance is of a rather complex type, although it is stated by Balls and by Kulkarni and Khadilker that the white-flowered (presumably the recessive) F_2 plants bred true, as in Kottur's cross between Asiatic cottons.

Harland[21] reviews the work of earlier investigators and presents the results of his own extensive study of the inheritance of petal color in crosses among members of the American group, representing a range from "cream" (the "white" of other students of this character) designated as grade 0, to deep yellow (grade 7). He concludes that cream is allelomorphic to any shade of yellow, with intensity of the color in the yellow class in F_2 showing much variation, due to the action of modifiers. The main factor (y) for absence of yellow is considered to be identical in Upland cottons and in the white-flowered Sea Island family but the latter, having had a yellow-flowered ancestry, possesses more plus modifiers for yellow than does Upland.

Certain Asiatic cottons have petals of a deep red color. Leake[36] crossing a red-flowered with a yellow-flowered Indian cotton, obtained results indicating partial dominance of red and a 3:1 ratio in F_2 if presence of red in any degree is contrasted with its complete absence. In Leake's cross between a red-flowered and a white-flowered Indian cotton, red was again partially dominant and the F_2 segregation suggests that combination of two dominant factors *R* (red), and *Y* (yellow), the former in double dose, may be required for the development of full red petals. (Kearney[27], p. 30.)

(To Be Concluded)

Lamarck

(*Continued from page* 308)

and distinguished himself for bravery in the few engagements in which he participated—which was prophetic of the courage with which he upheld his evolutionary theories in the later years of his life. Forced by illness to abandon a military career he took up the study of medicine, and in spite of lack of funds he was able to complete the four-year course. During this time he met Rousseau, who turned his interest in botany into a determination to make science his life work.

Lamarck's life was dramatic and tragic. Decorated for bravery in battle in his teens, a student of medicine at twenty,—a distinguished botanist, author of the *Flore Francaise*, and member of the Academy of Sciences at thirty-five,—a moving spirit in the establishment of the Jardin de Plantes and the Museum d'Historie Naturelle (which are still centers of biological research in France) before he was fifty, he nevertheless found time for speculations on physical science, and for taking an active interest in geology and palaeontology. Then at an age when many lives are nearly finished, he was forced to begin again as Professor of Zoology in charge of the collection of invertebrate animals. Within seven years he had made important contributions to the classification of the invertebrata and had published the first volume of his monumental *Animaux sans Vertèbres*. In 1801 his first views on evolution were published and these developed in *Philosophic Zoologique*, which appeared in 1809.

Throughout his life he was borne down by extreme poverty. He married four times, and had seven children of whom he lost three. The last ten years of his life were saddened by blindness. His greatest systematic work, *Animaux sans Vertèbres*, would never have been finished had it not been for the devotion of his eldest daughter, who under her blind father's directions completed the sixth and seventh volumes, which appeared in 1822. Old, blind, and almost abandoned by his friends, Lamarck died on December 28, 1829. It is a sad commentary that in spite of his position in the scientific world of Paris, he was buried with scant ceremony in an unmarked grave, or rather trench, in the cemetery of Montparnasse. His bones were later removed and consigned to the catacombs of Paris.

The picture reproduced on the cover was engraved in 1824, after Lamarck had become blind. We are indebted to Science Service for the loan of the print used in making the cut. Further details of Lamarck's life and work may be obtained from *Lamarck, the Founder of Evolution,* by Professor A. S. Packard. Longman, Green & Co., New York, 1901. This contains extensive translations of Lamarck's writings on the subject of evolution and heredity.